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7 JUL 1953

# THE DEER OF THE WEYBOURN CRAG AND FOREST BED OF NORFOLK

A. AZZAROLI

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THE BRITISH MUSEUM (NATURAL HISTORY)
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## GEOLOGY

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# THE DEER OF THE WEYBOURN CRAG AND FOREST BED OF NORFOLK

BY
AUGUSTO AZZAROLI
(University of Florence)

BRITISH MUSEUM
NATURAL HISTORY

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# THE DEER OF THE WEYBOURN CRAG AND FOREST BED OF NORFOLK

*By* A. AZZAROLI

(University of Florence)

## SYNOPSIS

The systematics of the Cervidae and the stratigraphy of the fossiliferous Pleistocene deposits of the Norfolk coast are clarified by a revision of material mainly in the A. C. Savin collection, in the British Museum (Natural History), and the John Gunn collection, in the Castle Museum, Norwich. Three successive faunas are distinguished in the Forest Bed Series. The nomenclature and relationships of various other fossil deer are also considered.

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## INTRODUCTION

A REVISION of the Forest Bed deer has been needed for a long time. The descriptions of the most interesting specimens are scattered in the older literature: Falconer (1868), Dawkins (1887), Newton (1882), Gunn (1891), Harmer (1899). A few specimens were described more recently by Reynolds (1929–34), but these works refer mainly to the antlers, and no comprehensive study has been published. Moreover the series in the British Museum (Natural History) has been considerably enriched through the careful and long-continued work of A. C. Savin (1861–1948) of Cromer; his first collection was acquired by the Geological Department in 1897, and his second in 1945.

The material examined consists of several hundred specimens, mostly in the Savin collection. I have further studied the important collection made by John Gunn (1801—1890), now in the Castle Museum at Norwich. There are in addition a few fossils of various origins in the two museums mentioned, in the Museum of the Geological Survey, in the Natural History Museum at Ipswich and in the private collection of Mr. J. E. Sainty of West Runton. I have not seen the material of other private collections, described by Dawkins (1887).

The fossils are highly mineralized, hard, and generally have a peculiar dark brown colour and a shiny surface; some of them, belonging to the older faunal elements (see later), are more ferruginous. Some are much worn, but for the most part they have a well-preserved surface. However, they consist almost exclusively of isolated bones. Only the skull of *Megaceros verticornis*, described as *Cervus belgrandi* by Harmer (1899), was found in connection with the first two vertebrae. This specimen is also exceptional in that the upper portions of its antlers are present. In the other specimens only the more resistant lower parts have been preserved. Most of them consist of lower portions of antlers, frontals, horizontal rami of mandibles, isolated teeth, limb bones and vertebrae. Brain cases are not uncommon, but no facial portions of skulls have been preserved, and maxillae are rare. Humeri and scapulae are represented only by the lower portions, except a heavy humerus of *Libralces reynoldsi*.

In the text I have used the abbreviations B.M. (G.D.) for the British Museum (Natural History), Department of Geology; G.S. for the Museum of the Geological Survey of England. The registered numbers of the specimens, when quoted in the explanations of the figures have not been repeated in the text. British Museum numbers preceded by the name Savin refer to his second collection.

### *Acknowledgments*

I am greatly indebted to Dr. A. T. Hopwood of the British Museum for having suggested to me the subject of this study and for his invaluable assistance in my

work. I wish to thank also Mr. W. N. Edwards, Keeper of the Geological Department of the British Museum; Miss G. V. Barnard, formerly Curator of the Norwich Museum; Dr. C. J. Stubblefield, Chief Palaeontologist of the Geological Survey, and Mr. H. E. P. Spencer, Curator of the Museum at Ipswich, for having kindly given me facilities for studying their collections; Mr. J. E. Sainty of West Runton, who led me in a field trip on the Norfolk coast; and Dr. K. P. Oakley (London), Prof. W. B. R. King (Cambridge), Prof. F. E. Zeuner (London), Prof. I. M. Van der Vlerk (Leiden) and Dr. R. Lagaaij (Leiden) for their criticism of the chronological section of this work.

## GEOLOGY

### *The Weybourn Crag and Forest Bed Series of the Norfolk Coast*

The Weybourn Crag and Forest Bed series, described in Reid's classical memoir (1890), is exposed at the foot of the cliffs along the Norfolk coast for some miles east and west of Cromer, and the Forest Bed is exposed also over a short distance around Pakefield, near Lowestoft. The cliffs consist of incompetent rocks—marine and freshwater gravels, sands and clays overlain by glacial drift, the whole resting on a levelled surface of chalk, and erosion is extremely rapid. The exposures continually change, and Reid's work is an invaluable record of many years of survey, at a time when the lesser development of coast defences made observation easier. Study of the stratigraphy is made difficult by rapid lateral changes, by breaks in the sequence, and by the discontinuity of outcrops. In many places the contorted glacial drift has disturbed this series, or cut it down to the chalk.

The marine and freshwater series, to summarize Reid's data, rests on the chalk. At the junction the surface of the chalk is covered by a " stone band " of large unworn or little-worn flints; this stone band represents no stratigraphical horizon. In the country around Cromer it is overlain by the " Weybourn Crag," a false-bedded shelly sand alternating with laminated clay. This crag generally occurs in patches on the stone band, beneath high tide-mark, between Weybourn and Trimingham. It " has been traced continuously from Cromer to Weybourn, except for short distances, where it is cut out by channels of the estuarine Forest Bed, or has been ploughed out by glacial action, so that the Boulder Clay rests immediately upon the Chalk " (Reid, 1890: 139). In a section at East Runton it yielded a rich fauna of molluscs and some mammal bones. In isolated outcrops its distinction from the Forest Bed is sometimes difficult, so that many authors overlooked its occurrence. Towards the south-east the Weybourn Crag becomes more clayey and probably passes laterally into the Chillesford Clay, which in this section of the coast has been found only in borings, at Mundesley and possibly at Happisburgh.

The Forest Bed series covers unconformably the Weybourn Crag and has always a more or less gravelly base. Probably there is a land surface between these two formations, " for in one place the Crag has a rather weathered appearance; but of this one cannot be certain" (Reid, 1890: 149).

The Forest Bed series is in three divisions: a " Lower Freshwater Bed," composed of carbonaceous clays, silt and loam; an "Estuarine Bed" or Forest Bed *sensu* *stricto*, composed of false-bedded carbonaceous sands and laminated clays with mammal bones and drifted tree-stumps; and an "Upper Freshwater Bed," composed of peaty clays and sands. The discontinuous Lower Freshwater Bed is very seldom preserved, and its observation to-day is still more difficult than at the time when Reid saw it on the shore north west of Cromer, where it cut through the Weybourn Crag (1890: 159), and at Trimingham (1890: 163). The Estuarine Bed is practically continuous. The Upper Freshwater Bed is somewhat variable in facies and its identification is not always easy. It also is discontinuous and is separated from the estuarine division by an eroded and deeply weathered surface.

### *The Occurrence of Mammals*

Many of the mammalian remains were found loose on the beach, especially after storms. Some, however, were actually extracted from the rock *in situ*. As a rule they were said to come from the Forest Bed, *sensu lato*, which is still considered the chief mammal-bearing horizon; but in the course of the present work it has become apparent that they are of different ages, so that their occurrence needs more careful discrimination. Most of the fossils I have examined were obtained by A. C. Savin of Cromer, who collected for more than fifty years and gave accurate indications in his catalogue. The specimens I have determined are said to come from the Forest Bed at W. Runton, E. Runton, Cromer, Overstrand, Sidestrand, Trimingham, Mundesley, Bacton, and Pakefield; from the beach at Palling and from the Upper Freshwater Bed at West Runton. A single specimen, a fragment of a lower jaw of *Megaceros dawkinsi*, is said to come from the Weybourn Beds at Weybourn. The specimens from other collections were all stated to come from the Forest Bed, partly from the same localities as Savin's, partly from other localities, such as Ostend, Happisburgh, the Walcot gap, and Hopton. However, not seldom there is only the indication "Forest Bed; Norfolk." A few specimens were dredged off the coast and on the Dogger Bank.

It is remarkable that Savin did not distinguish an Upper Freshwater Bed in many localities where it has been recorded by Reid; possibly he was misled by differences in facies from the corresponding bed at West Runton, and as a matter of fact the distinction of these horizons in the field is not always easy. Savin distinguished a Lower Freshwater Bed at East Runton, and Weybourn Beds at East Runton and West Runton, but recorded from them only fish remains. Here too he was probably misled by the common belief that mammal remains occurred only in the Forest Bed and Upper Freshwater Bed. But, as stated above, Reid found mammal bones also in the Weybourn Crag, at East Runton. Finally, Savin's attribution to the Weybourn Crag of a lower jaw from Weybourn might be based merely on the locality and might be equally incorrect.

The mixed character of the "Forest Bed Fauna" led me to suppose that its members came from different horizons. The characters of the fossils, consisting of large and well-preserved antlers of deer, rules out any possibility that they were washed in.

The distribution of the species I have studied shows that there is no sharp break between the fauna of the estuarine Forest Bed and that of the Upper Freshwater Bed, which, according to my correlations, belong to the great Mindel-Riss interglacial (see later, section " Chronology "), whereas an older fauna may be sharply distinguished. There is no doubt that it came from an older horizon, separated from the estuarine bed by a remarkable gap. The widespread occurrence of this fauna, as well as the high ferruginous content of most of its specimens, rule out the Lower Freshwater Bed, whilst the Weybourn Crag corresponds to what may be expected to be their matrix. In fact, most of Savin's specimens are said to come from the gravel pans and sands on the shore, at some distance from the cliffs; and Mr. Sainty of W. Runton has in his private collection a beautiful lower jaw of *Libralces gallicus*, a typical representative of this earlier fauna, which he extracted from a patch of shelly crag directly overlying the stone band, on the shore between West Runton and East Runton, below high tide-mark. This crag, still occurring in patches but variously exposed owing to the rapidity of erosion, corresponds to Reid's description of the Weybourn Crag.

Boyd Dawkins, who certainly was not influenced by prejudices about the stratigraphy, referred a skull of the same species from the Savin collection (1887, pl. 1, fig. 1) to the " Weybourn Beds (Forest Bed Series), East Runton, Cromer." Savin's catalogue gives for this specimen the sole indication " East Runton Forest Bed."

These older species were found only in the western section of the coast, between Sidestrand and West Runton, where the Weybourn beds are exposed. Very few specimens came from Mundesley, where the Chillesford Clays are concealed beneath the beach.

## THE PHYLOGENY OF THE CERVIDAE

The early history of the deer is little known. Probably they achieved the greater part of their evolution in Asia and North America, where the record is fragmentary and very scanty, during the Pliocene. In Europe their history is largely one of successive waves of immigration and replacement. Their classification is therefore vague. Simpson (1945) did not give an exact picture of the phyletic relationships: for instance, his *Odocoileinae* are not a phyletic unit, neither are his *Cervinae* except in so far as living species are concerned.

In practice only restricted groupings of related genera can be established; the precise rank of these higher taxonomic units is largely a matter of taste. They may be called without prejudice subfamilies. Among the living deer seven subfamilies are recognized: *Cervinae, Muntiacinae, Odocoileinae, Capreolinae, Rangiferinae, Alcinae, Hydropotinae.* As yet hardly any other taxonomic categories within or above these subfamilies can be established, and if we take into account also the fossil forms, things become more difficult.

The present work is concerned only with the *Cervinae, Capreolinae* and *Alcinae.*

### *The* Capreolinae *and* Alcinae

The history of the *Capreolinae* is quite obscure. Some Miocene forms have been tentatively referred to this group, but they are poorly known (Azzaroli, 1948:

46 ff.), and, so far as I am aware, there is no record of this subfamily during the Pliocene. The dental characters vaguely suggest some affinity with the *Alcinae.*

The *Alcinae* are represented in the Quaternary by three genera, *Alces, Cervalces* and *Libralces*, closely similar in the characters of the dentition and limb bones, but widely divergent in the skull. They are practically unknown in the Pliocene, but were already differentiated in the Pontian, where they are represented by *Alces maeoticus.*

### *The* Cervinae

The problem of the *Cervinae* is less simple, and requires more explanation. In 1948 I stated that they were derived from the Pontian *Pliocervinae* of S.E. Europe and China; the definition of the *Pliocervinae* was based on Zdansky (1925, 1927). A study of the works of Alexejew and Khomenko on the Pontian deer of S.E. Europe necessitates some modification of this statement.

### (a) *The Pontian deer from S.E. Europe*

In 1913 Alexejew named *Procervus variabilis* from Pontian deposits near Petroviêrovka, S. Russia. A more complete description followed in 1915. This species is distinctly smaller than a fallow deer; its teeth are brachyodont, the upper molars have a discontinuous cingulum, and the lower molars a well-developed *Palaeomeryx*-fold. Varying with the individual, $P_4$ is either primitive or advanced; the upper premolars are primitive and the upper canines relatively strong. The skulls are badly damaged but seem to be of a primitive, rather unspecialized type. The brain cases are long, the supraoccipital crests weak. The pedicles are set obliquely and form two ridges at the sides of the forehead. The antlers, of various ages, are short, stout and much flattened; their form is irregular and extremely variable. They consist of a flattened, very strong brow tine, sometimes bifurcated at the top; and a short beam, gradually expanding upwards into a narrow palmation, ending in two to six small tines. The surface is deeply grooved. The first bifurcation takes place near the burr and eventually a small accessory tine is given off from it. The antlers of younger individuals are forked, and in the first stage they consist of simple prickets. The limb bones are primitive. The shaft of the ulna is strong, the upper epiphyses of the radius and tibia are small, and the fore limb has complete lateral metacarpals, with a well-developed articulation for the corresponding toes.

In 1914 Khomenko published a description of some Pontian deer from Taraklia, Bessarabia. His material was scanty and fragmentary, nevertheless he founded on them three new genera and species, *Cervavitus tarakliensis*, *Cervocerus novorossiae*, *Damacerus bessarabiae*, based on antler characters. Khomenko's specimens also included some teeth; they showed slight differences which he supposed to be specific characters. On these three genera Khomenko founded his new subfamily *Pliocervinae.*

Khomenko's genera have been variously accepted. Zdansky (1925) supposed that *Cervocerus novorossiae* and *Damacerus bessarabiae* were synonymous; Simionescu & Dobrescu (1941) accepted the specific distinction only, and determined other specimens from Bessarabia as *Cervocerus bessarabiae.* Simpson followed these authors and recognized the genera *Cervavitus* and *Cervocerus,* and included *Damacerus* in the latter.

However, there is little doubt that Khomenko's genera and species are all synonymous. The differences between the antlers are due to growth stages, and the teeth do not differ by more than individual characters. The choice for the generic and specific names is thus open, and here we shall adopt *Damacerus bessarabiae.* Its holotype is the antler figured by Khomenko (1914, pl. 4, fig. 6), the only one of Khomenko's specimens that is fully grown.

The deer from Petrovièrovka is closely related to this. The teeth are indistinguishable; $P_4$ displays the same fluctuations. The frontals, too, seem to be very similar, and the only marked differences lie in the antlers. In *Damacerus bessarabiae* they are less flattened, the brow tine is smaller and the first bifurcation is set high above the burr. It is consistent therefore to attribute these two species to the same genus. *Procervus* is preoccupied and the valid name is *Damacerus,* which will include therefore two species, *D. bessarabiae* (the genotype), and *D. variabilis.*

### (b) *The Pontian deer from China*

In 1925 and 1927 Zdansky identified with Khomenko's *Cervocerus novorossiae* some deer of various Pontian localities in China. Other specimens from Shansi were referred to the same species by Teilhard & Trassaert (1937). These identifications are incorrect. The Chinese deer show only superficial similarities to those of S.E. Europe, but at the same time they display differences showing that they belong to completely different lineages.

The Chinese so-called *Cervocerus novorossiae,* as defined by Teilhard & Trassaert [Zdansky's description is sometimes vague and partly contradicted by his figures; moreover some of his attributions are questionable (see Teilhard & Trassaert, p. 38)], is a species of slightly larger size than the European *Damacerus.* Its skull is rather primitive; the pedicles form two prominent ridges on the sides of the forehead. The lacrimal pits are large and deep. The antlers are three-tined, cylindrical, and display a great variability in the position of the first bifurcation and in the length of the beam. Teilhard & Trassaert distinguished a " short type," with a straight beam, and a " long type," with a gently curved beam; they are linked by intermediate forms. The dentition is brachyodont. $P_4$ is primitive and there is no trace of the *Palaeomeryx*-fold on the lower molars. The upper premolars have the inner wall split, and a strong cingulum is stated to occur in the upper molars, but this is not to be seen in the figure. There are two complete but very thin lateral metacarpals, with rudimentary epiphyses.

With the possible exception of some more flattened antlers (pl. 5, figs. 1, 2), Zdansky's *Cervocerus novorossiae* corresponds on the whole with this species. According to him the cingulum is variable in the upper molars, and in the lower molars he described what he regarded as the remnants of a *Palaeomeryx*-fold: " Es handelt sich meistens um eine, vorn mehr oder weniger scharf begrenzte Rinne. An nur ganz wenigen Zähnen ist eine solche nicht zu konstatieren." This is somewhat vague, but there is certainly no typical *Palaeomeryx*-fold, and no trace of it can be seen in the published photographs.

Zdansky also included in the *Pliocervinae* the genus *Procapreolus* Schlosser, the validity of which has been questioned by Teilhard & Trassaert. The latter authors, on the other hand, described a *Cervavitus demissus* whose generic identity with the European forms is no less questionable.

### (c) *The relationships of the Pontian* Cervinae

In conclusion, in the Pontian, apart from some smaller forms more or less closely related to the *Muntiacinae*, and from the *Alcinae*, the *Cervidae* were already represented by two well-differentiated groups, namely the European *Damacerus*, with two species, and the Chinese three-tined deer, seemingly belonging to one species, for which new generic and specific names are required. They differed in the characters of the antlers, of the dentition, and of the fore limbs. These characters enable us to make some partly hypothetical inferences about their relationships.

In its dental characters the European *Damacerus* is closely related to the two-tined Miocene deer, and may have been derived from a genus with a well developed burr, e.g., *Euprox* (for full references on Miocene deer see Stehlin, 1939, with bibliography).

In my opinion the value of the *Palaeomeryx*-fold has been underestimated. It is supposed to have gradually disappeared by the end of the Miocene, but there is no evidence for this assumption. Throughout the Miocene it does not show any tendency to become reduced or to fluctuate, and it is still uncertain whether it has really vanished, or has been wiped out by the extinction of the species that bore it. A solution to this question might possibly be afforded by *Cervus ramosus* Croizet & Jobert (1826–28, fasc. 5, pl. 5, fig. 2). The age of the type is uncertain, but the same species occurs in the Villafranchian of St. Vallier-sur-Rhône and of Villaroya ; there is no trace of the *Palaeomeryx*-fold in its lower molars. A more primitive variety, *Cervus ramosus* var. *pyrenaicus*, which might perhaps be the ancestor of the typical form, was described by Depéret (1897 : 99–112, 124–125) from the Upper Pliocene of the Roussillon. Among the many lower jaws which can be attributed to this variety, there are specimens with a distinct *Palaeomeryx*-fold and specimens without any trace of it. I am unable to state whether there are intermediate conditions, nor whether all these jaws belong to the same species ; this however is highly probable, because the other deer from the Roussillon (Depéret's *Capreolus australis* and *Capreolus ruscinensis*, but actually belonging to one species) are much smaller. If so, *Cervus ramosus* would afford a good example of the *Palaeomeryx*-fold disappearing by fluctuation.

In the three-tined Pontian deer from China there was no *Palaeomeryx*-fold. $P_4$ was more primitive than in the European deer of the same age; the upper premolars were rather molarized, but this character always seems to be very variable and its significance is not quite clear.

This is all that is known of the Upper Miocene ancestors of the *Cervinae*. A large part of them very probably originated from the Chinese species, and the lineage represented in the Pontian of S.E. Europe may possibly have survived with *Cervus ramosus* up to the Lower Pleistocene.

### (d) *The Pliocene and Pleistocene* Cervinae

The history of the *Cervinae* during the Pliocene is obscure. Besides *Cervus ramosus* and its small relative from Roussillon, which might be related to *Damacerus*, several species of quite uncertain affinities are known. Most of them were found in the Montagne de Perrier and other localities of France. There is no evidence that any of them survived into the Pleistocene.

It would be consistent to give each lineage a distinct generic name, but the use of the name *Cervus*, although improper, cannot be dispensed with as long as these species are so poorly known. However, the name *Anoglochis*, originally proposed by Bravard, Croizet & Jobert, might perhaps be adopted for *Cervus ramosus*.

At the beginning of the Quaternary we find that the various genera which compose the subfamily are already differentiated, although in many cases represented by relatively primitive species. *Euctenoceros* and *Megaceros* make their first appearance in the Red Crag of East Anglia, *Euctenoceros* also in the Dutch Poederlian (see later), *Dama* in the Villafranchian of Tuscany (Azzaroli, 1948), *Rucervus* in the Pinjor stage of the Siwalik hills (to be described in a forthcoming paper by the author), *Rusa* in the Sanmenian of Nihowan (Teilhard & Piveteau, 1930), *Sika* in Chouk'outien and other Pleistocene localities (Young, 1932), *Axis* in the Lower Pleistocene of Shansi and Java (Teilhard & Trassaert, 1937; Stremme, 1911); *Cervus* s.str. makes its first appearance in the second interglacial of Europe. *Elaphurus* is doubtful in the Sanmenian of Nihowan, but has been identified in the Pleistocene of Japan (Matsumoto, 1915), and is represented also by a subfossil species at Anyang, N. Honan (Teilhard & Young, 1936). *Przewalskium* alone is not known as a fossil. There are in addition some primitive and poorly known species which cannot be fitted into any of these genera: " *Cervus* " *rhenanus* from Tegelen, " *Cervus* " *perolensis* from the Auvergne (Bout & Azzaroli, 1953), " *Cervus* " *punjabensis* and another species from the Upper Siwaliks (to be described in a forthcoming paper), and " *Cervus* " *philisi* from Sénèze (Schaub, 1942).

Many of these genera and species may have been derived from the Pontian three-tined deer of China; but some highly divergent genera, as, e.g., *Elaphurus* and *Megaceros*, are very probably of a quite different origin.

## THE DEVELOPMENT OF THE ANTLERS

### (a) *General Considerations*

Much has been written on the growth of the antlers, but our knowledge on this point is not entirely satisfactory. Each species and genus has its own peculiar pattern of antlers, obviously determined genetically, but the mechanism by which this pattern is brought into existence is practically unknown. Wislocki and others (1946, 1947) have studied the innervation and the process of ossification. It has been established that the form of the antlers is not influenced by the course of nerve fibres, and attempts to explain the form of the antlers by the course of blood-vessels (see literature in Wezel, 1949) are equally unsatisfactory. Moreover the antlers display an individual variability of form and size that cannot be explained by the action of genetic factors alone. There is evidence that more factors, partly genetic, partly purely mechanical, influence the determination of their form. Huxley (1932) established that their size is controlled by a complicated allometric law, varying from species to species. It is known, too, that increase in size of the antlers, within a species or subspecies, is followed by a more complicated ramification. Inasmuch as this phenomenon occurs among individuals of the same genetic constitution, or even in successive growth stages of the same individual, it cannot be because of genetic differences, but rather because of purely mechanical factors: the antler tissue, growing from the top of the pedicle, seems to be unable to develop indefinitely in cross-section, but tends to divide as soon as it has reached a certain limit of bulk. A closer study of this phenomenon is obviously outside the province of palaeontology.

In the recent deer, division generally takes place dichotomously, with the first bifurcation or bifurcations in a nearly longitudinal plane. This led Pocock (1933) to formulate his theory of dichotomous growth; but it may be shown that this law is not general.

Each species obviously has its own range of variation, and eventually its particular type of asymmetry, as, e.g., the reindeer. Broadly, the species with more complicated antlers are also the more variable. Very much has been written on the variability of antlers, especially of the red deer; one of the most recent accounts has been given by Wezel (1949). Allowance must however be made for the unnatural conditions under which red deer very often live (inbreeding, artificial selection, unfavourable or exceedingly favourable environment). In deer living under natural conditions the range of variation is not so wide.

### (b) *History*

If we trace back the history of the deer we may form a mental picture of the primitive conditions of the antlers, and of the way the more advanced features gradually became established.

No continuous phyletic line of an appreciable length has yet been ascertained. The principle of parallel evolution, recently exposed and discussed by Merla (1949: 117 ff.), will be extensively applied here. This implies the more general principle of evolution controlled by internal factors, the validity of which has been questioned by many recent authors who hold a purely "Darwinian" point of view. The reasons for the interpretation accepted here have been discussed at length by Merla (1949) and by Watson (1949).

In my opinion the principle of evolution directed by internal factors is the only one to give a satisfactory explanation of the phyletic development of antlers. It could be argued that their development might be controlled by factors linked with characters under selective control; this interpretation however gives no explanation for the numerous instances of parallel evolution, nor for the polymorphism of antlers, which is in striking contrast with the uniformity of the other body characters.

Apart from the evolution of antlers, there are not many clear examples of ortho-evolution of characters which are surely not under selective control. A spectacular exception is the pachyostosis of the skull of *Megaceros*.

### *Lower and Middle Miocene: the primitive antlers*

True *Cervidae*, shedding their antlers, made their first appearance in Europe during the Burdigalian and remained very primitive during the Helvetian and Tortonian (for full reference see Stehlin, 1939). They form a polymorphic group. Complete and well-preserved skulls are not known, but great differences are displayed in the position of the pedicles, and in many cases there is no typical burr. But one common feature is apparent: the antlers never grow in the form of prickets. Even in the earliest stages they tend to divide, taking the form of an irregular crown (*Stephanocemas*; in fact the form is somewhat intermediate between a crown and a fork), a fan (*Palaeoplatyceros*) or a longitudinal fork (*Heteroprox*, *Dicroceros*, *Euprox*). In Asia some of these forms survived into the Pliocene, and may perhaps have given origin to the living *Muntiacinae*.

### *Pontian. The emergence of modern types*

A trend towards the formation of a beam became apparent in the Pontian. *Amphiprox*, from Eppelsheim, was still very primitive, with short antlers consisting of a straight beam and a very small brow tine, branching off high above the burr; but at the same time, deer with more complicated antlers lived in the S.E. of Europe and in China. They all had a distinct burr and a branched beam.

*Damacerus* is probably closely related to the earlier European deer. *Damacerus variabilis* seems to represent the most primitive condition. The differentiation between brow tine and beam is not very well established: they are both flattened, the brow tine is relatively large and bifurcated at the top. The general form of the antlers is very variable and irregular. The antlers of young individuals consist of prickets, but it is questionable whether the ontogenetic development actually reproduces the phyletic history. The formation of the pricket might be due to the action of genetic factors, normally leading to the formation of the beam, which in the youngster are not counterbalanced by a sufficiently strong tendency towards ramification, owing to the small size.

*Damacerus bessarabiae* is more advanced. There is a typical beam and a much smaller brow tine. The first bifurcation is set rather high above the burr, and in my opinion this should be considered an advanced character. The point, however, is not quite clear, and palaeontological evidence of the evolution of later forms (see, e.g., *Dama nestii nestii* from Olivola and the Upper Valdarno; Azzaroli, 1948) may seem to contradict this assumption. As a matter of fact, genetic and mechanical factors trending in opposite directions interact. The upwards shift of the first bifurcation is determined genetically, and the downwards shift during ontogenetic development is certainly due to a purely mechanical factor, the larger bulk of growing tissue inducing earlier bifurcation. This factor also may eventually act in phyletic evolution. Moreover, a third character, namely, the opening of the angle of the bifurcations, seemingly under genetic control, may also interfere; this, however, seems to have become felt only after the end of the Miocene.

In the three-tined Pontian deer of China the antlers consisted of a cylindrical beam and cylindrical tines. They are rather variable, both in length and in the position of the first bifurcation. It has been stated in the preceding section that some palmated antlers figured by Zdansky might perhaps belong to another species.

### *Pliocene and Quaternary. New evolutionary trends*

Although the antlers of these primitive deer were relatively small and simple, they were very variable. No attempt will be made here to explain this, but in later forms the patterns of antlers became more constant. New features appeared, as bifurcations at an obtuse angle, helicoidal tortion and undulation of the beam and tines, peculiar types of spatial arrangement of the branches (e.g., on a spherical surface in *Rucervus*, on a plane in *Euctenoceros*), or branching of the tines.

The flattening of the beam and tines is a very common feature. In some cases it may be a secondary appearance, but its phyletic origin is not always clear. This is true also of the palmation. In some instances, e.g., *Alces alces*, no sharp distinction can be traced between palmated and non-palmated antlers.

## (c) *On the Homologies of the Tines*

The discussion of the formation of antlers leads to the question of the homologies of the tines. Some words on this problem are necessary because too rigid an interpretation of the homologies would be misleading.

After considering the work of other authors, Pocock (1933) proposed an interpretation of the homologies based on the theory of dichotomous growth. This can be summarized as follows. The primitive condition is assumed to be represented by the pricket. In the next stage it divides into an anterior and a posterior tine ($a^1$ and $p^1$). These two tines may have the same potentiality of growth and further division: this happens, e.g., in *Elaphurus* and *Blastocerus*. But generally $p^1$ is the stronger and divides into $a^2$ and $p^2$; then $p^2$ divides into $a^3$ and $p^3$, etc. In accordance with this principle Pocock established the homologies between the tines of all the living genera of the *Cervidae* and many fossil forms. In the particular instance of the red deer the bez tine normally occurs but is not constant; this was interpreted as having originated from the division of the brow tine.

In 1948 I fully accepted Pocock's views, but I now realize that rigid application of them is not possible. This theory however has the merit of having shown that there is no fundamental difference between beam and tines.

It has been shown above that the pricket is not the primitive condition, and that in the earliest stages branching is more or less irregular. As a matter of fact at the beginning the tines have no morphological individuality, that is, they cannot be compared to an organ such as a tooth. What is inherited is the general pattern of antlers. As this pattern gradually evolves, the beam and the tines acquire a certain degree of individuality, which, however, is not absolutely fixed. The evidence for this is that the eventual suppression of a tine, or the presence of accessory tines or even an accessory beam (a not uncommon occurrence in the red deer and reindeer), does not alter the fundamental pattern of the antler. The example of the tamin (Fig. 1) is also instructive. In this species, the surface of the antlers is sometimes very scabby; the tines (except of course the brow tine) are small, and no sharp distinction can be traced between the smaller tines and the larger asperities of the surface.

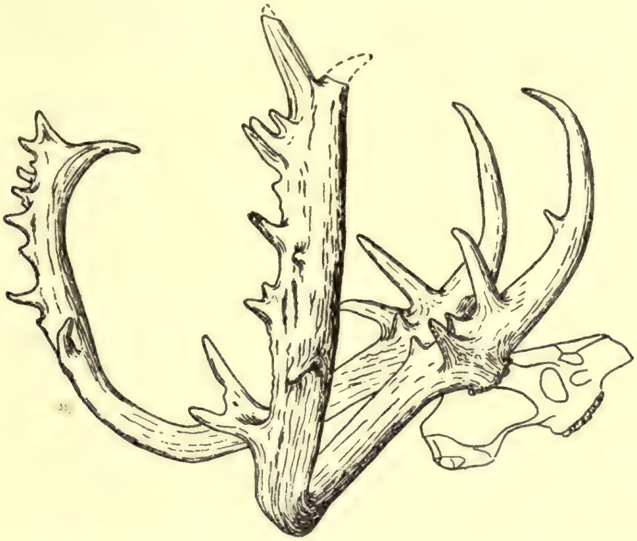

FIG. 1. *Rucervus eldi.* B.M. (Zool. Dept.), no locality. $\frac{1}{8}$ natural size.

True homologies can be established only between related forms, in which the evolution of the antlers has followed the same path. It is meaningless to argue whether the homologue of the brow tine of, say, a fallow deer is represented by the small inner tine of *Odocoileus*, or by its bifurcated anterior tine, which in turn is obviously homologous with the anterior tine of *Blastocerus*; or to look for the homologue of the bez tine of the red deer in the reindeer and in the giant deer.

## SYSTEMATIC DESCRIPTIONS

### Genus *LIBRALCES* Azzaroli

In another paper (1952) I have established the new genus *Libralces*, with genotype *L. gallicus* from the Upper Villafranchian of Sénèze. This species is present also in the Lower Quaternary of the Norfolk coast, together with three other species of the same genus. These are more imperfectly represented, and are distinguished mainly by their size. The distinction of the dentitions is easy, but greater difficulties arise in determining other remains, for the most part imperfect fragments of skulls and antlers. The attribution of some of them will therefore remain uncertain. The limb bones that can be attributed to this genus are scanty.

I have defined the genus *Libralces* as follows (1952 : 134): skull broad, depressed and heavily built; forehead broad; antlers palmated, with a long beam directed horizontally outwards and gently curved. Nasals long, articulated with the premaxillae. Upper canines presumably present in the genotype, molars and premolars brachyodont, lower molars with strong basal columns; traces of the *Palaeomeryx*-fold in $M_1$, eventually also in $M_2$; $P_4$ as in *Alces*. Forelimb telemetacarpal, size large.

### ***Libralces gallicus*** Azzaroli

(Figs. 2, 3, 4 B, 5 A, 9 B, 10 D.)

1887. *Alces latifrons* (Johnson) Dawkins (pars), p. 1, pl. 1, figs. 1, 3 ?, 5.
1931. *Alces latifrons* (Johnson): Roman & Dareste, p. 1256.
1944. *Alces latifrons* (Johnson): Schaub, p. 285.
1952. *Libralces gallicus* Azzaroli, p. 134.

#### *Summary Description of the Holotype and Paratype*

The type of this species, a complete skeleton of a full-grown male, and a second incomplete skeleton were found in the Upper Villafranchian of Sénèze. The original description may be summarized as follows: A species of large size, but distinctly smaller than the living elks. The skull is broad and depressed, with a broad forehead and a very thick roof. The face is proportionately less developed than in *Alces* and is characterized by the long nasals, which are articulated with the premaxillae. The lower molars bear well-developed basal columns, and the first lower molar has a distinct groove on the hinder surface of its antero-external crescent. The antlers consist of a long, slender beam, directed horizontally outwards and gently twisted, which ends in a small palmation, set obliquely to the axis of the body, with small tines on its edge like *Alces alces*. The limb bones are slender and differ from those of *Alces* only by their smaller size. The neck is relatively long.

#### *The Specimens from the Norfolk Coast*

OCCURRENCE. All the specimens that can be identified with certainty were found at East Runton and Sidestrand. Imperfect specimens, whose identification is somewhat doubtful, were found at West Runton, Cromer and Pakefield; the last are much rolled.

DESCRIPTION. The best specimen is represented by a brain case with its left antler, originally figured by Dawkins (1887, pl. 1, fig. 1). In Azzaroli (1952, pl. 15, fig. 2) and in Fig. 2 the antler has been omitted. An adult, or nearly adult antler from Sidestrand (Dawkins, 1887, pl. 1, fig. 5) and two antlers from East Runton can also be attributed to this species. All these specimens show a rather narrow range of variation. The more robust antlers (Fig. 5A, and Dawkins' fig. 1) tend to develop shorter beams.

A second brain case (Fig. 3), mentioned also by Dawkins, very probably belongs

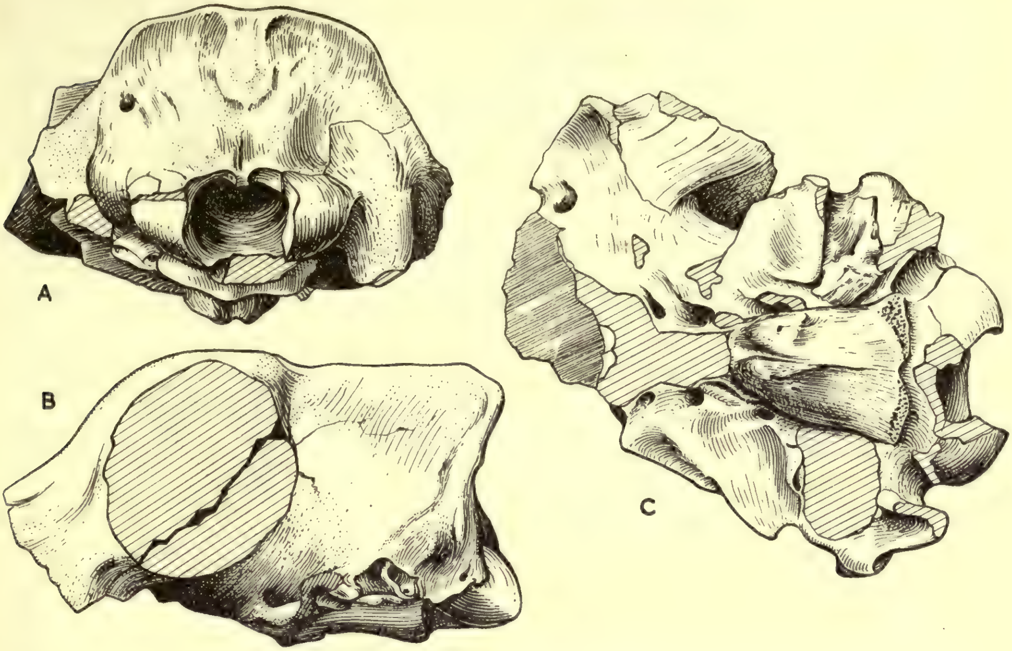

FIG. 2. *Libralces gallicus*, skull from East Runton. B.M. (G.D.), M. 6101. ⅓ natural size. (Specimen figured by Dawkins, 1887, pl. 1, fig. 1, and by Azzaroli, 1952, pl. 15, fig. 2.) A, occipital view; B, lateral view; C, basal view.

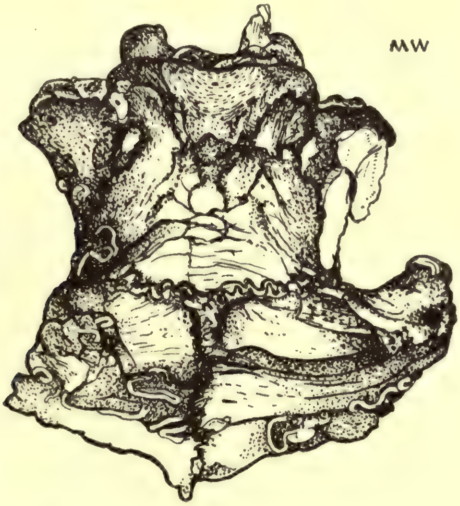

FIG. 3. *Libralces gallicus ?* Skull of a young specimen, dredged off the Dogger Bank. B.M. (G.D.), 46108. ⅓ natural size.

to the same species. It was dredged off the Norfolk coast and is highly mineralized, like the other fossils from the Weybourn Crag and Forest Bed. This brain case is smaller than the skull from East Runton, and nearly of the same size as the holotype. The sutures are open, giving evidence that it belonged to a young animal.

The correlation between the antlers, the brain cases and the teeth is made possible by comparison with the holotype. Two incomplete lower jaws from East Runton (Figs. 4 B, 10 D; Azzaroli, 1952, pl. 15, figs. 3, 4) and some isolated lower molars from Sidestrand may be attributed to this species.

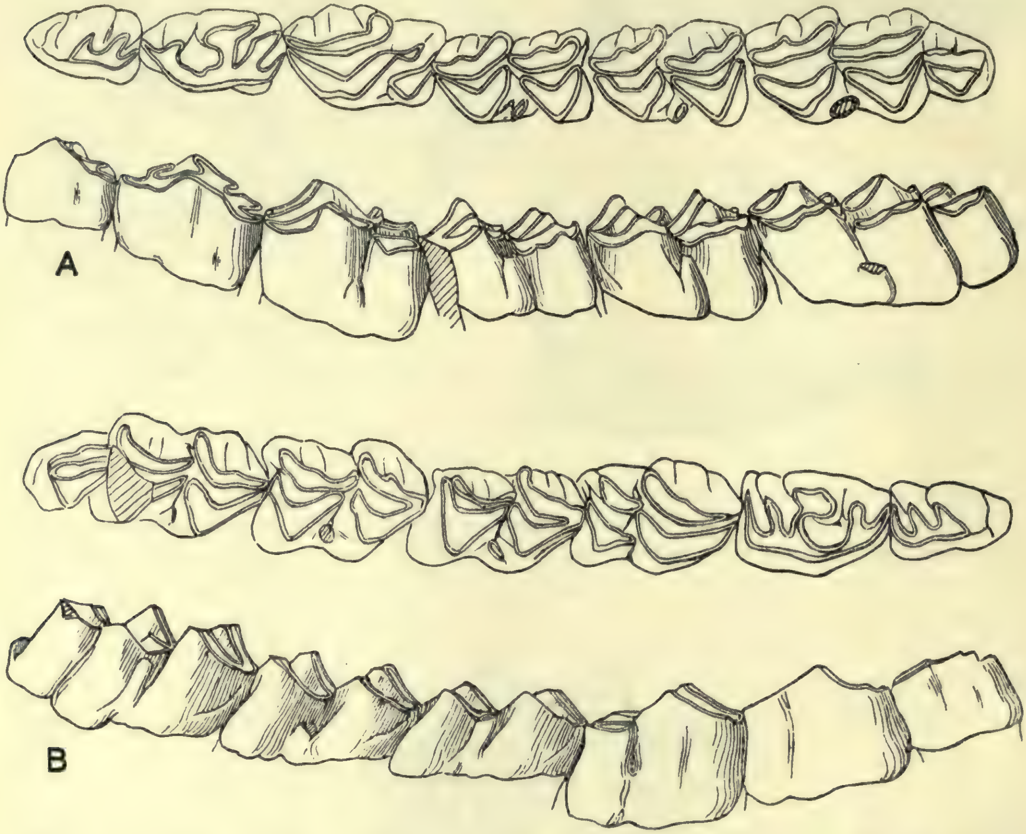

Fig. 4. A. *Libralces minor*, holotype. Lower dentition, no locality. B.M. (G.D.), M. 6227. B. *L. gallicus*, lower dentition, East Runton. B.M. (G.D.), M. 6206. Natural size.

A fine lower jaw in the private collection of Mr. J. E. Sainty of West Runton, recorded also above (section " Geology "), was extracted *in situ* from the Weybourn Crag between East Runton and West Runton.

The identification of more imperfect specimens from other localities will be discussed later.

MEASUREMENTS:—

| | E. Runton.<br>B.M. (G.D.) M. 6101 | Dogger Bank.<br>B.M. (G.D.) 46108 |
|---|---|---|
| Skull: | | |
| Occipital breadth | 164 | 145 |
| Occipital height | 107 | 99 |
| Minimal frontal breadth *ca.* | 212 | |
| Breadth of condyles | 82 | 69 |
| Parietal breadth behind the pedicles | 109 | 105 |

| | E. Runton<br>B.M. (G.D.) M. 6206 |
|---|---|
| Lower tooth-row: | |
| Total length | 136 |
| Length of the three molars | 80 |
| Breadth of $M_2$ | 19 |

## ***Libralces reynoldsi*** n. sp.

(Figs. 5 B, 6–8, 9 C.)

1891. *Alces* sp., Gunn, pl. 5, fig. 4.
1934. *Alces latifrons* (Johnson): Reynolds (pars), fig. 6*c*.

HOLOTYPE. B.M. (G.D.) M. 6553: a nearly complete brain case, with the left beam (Figs. 6, 9) figured also by Reynolds, 1933, fig. 6*c*. Mundesley.

ADDITIONAL SPECIMENS. In the British Museum: two very imperfect antlers, from Sidestrand and Mundesley; an imperfect humerus from Overstrand; a naviculocuboid from Overstrand; two phalanges, from Mundesley and Trimingham; a fragment of a lower jaw from Overstrand. In the Norwich Museum: a lower jaw, from Cromer; two imperfect antlers, the one from Trimingham (Gunn, 1891, pl. 5, fig. 4), the second dredged off the Norfolk coast.

DIAGNOSIS. A much larger species of *Libralces* than *L. gallicus*, remarkably exceeding also the size of *Cervalces scotti*. Skull and antlers more heavily built and relatively broader than in *L. gallicus*; other characters closely similar.

DESCRIPTION. *Libralces reynoldsi* differs from *L. gallicus* in its much larger size, and in some features obviously correlated with this character. The skull is similarly broad and depressed, and is distinguished by the stronger development of the supraoccipital and supratemporal crests; the latter have developed a distinct knob behind each pedicle. A close comparison between the skulls of *L. reynoldsi* and of *L. gallicus* shows that their proportions are not identical. The skull of the larger species is relatively broader: it exceeds that of the genotype by roughly $\frac{1}{4}$ in length and height, and by $\frac{1}{3}$ in breadth. The holotype of *L. reynoldsi* seems to have been an unusually large specimen; the diameter of its beam above the burr is 96 mm. In comparison with the strongest specimen of *L. gallicus* from East Runton (52 mm.), this gives a cross-section three times as large. Apart from the strong development of the supraoccipital crest, no external features intended to counteract the weight of the antlers are seen in the skull, but the thickness of the frontals, which are massive, measures 40 mm., exactly double that in the larger specimens of *L. gallicus*. The brain cavity is therefore remarkably small. In the holotype it is partly filled with the matrix, a hard sandstone impregnated with iron oxides.

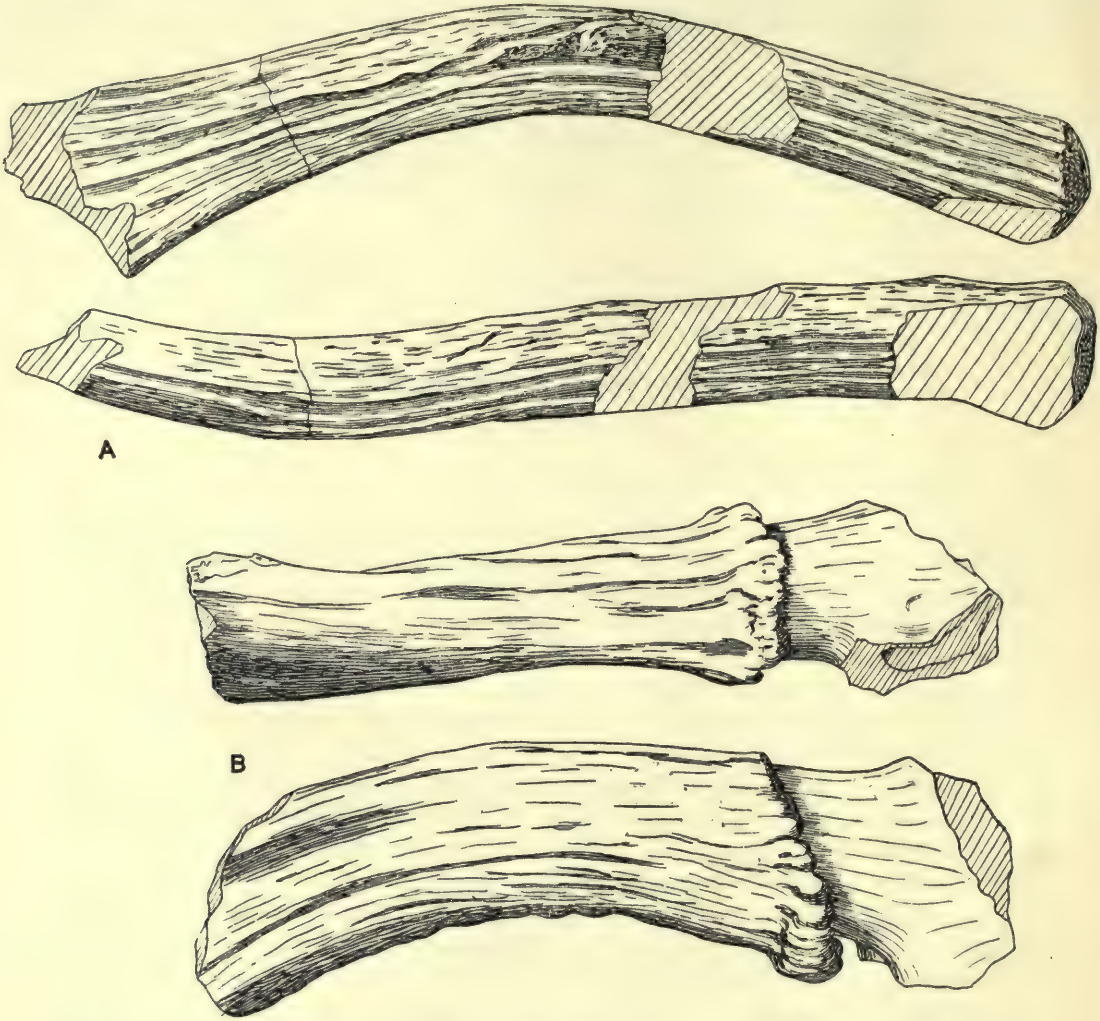

FIG. 5. A. *Libralces gallicus*, right antler from East Runton. B.M. (G.D.), M. 6554. B. *L. reynoldsi*, right antler from Mundesley. B.M. (G.D.), Savin 2223. ¼ natural size.

The remains of the antlers are very incomplete. Unless too much worn, they show a very strong burr and a deeply grooved surface; the beam is gently bent. In the holotype and in the antler of Fig. 5 B, which are the largest specimens I know and presumably belong to the same individual, the beam is short and the

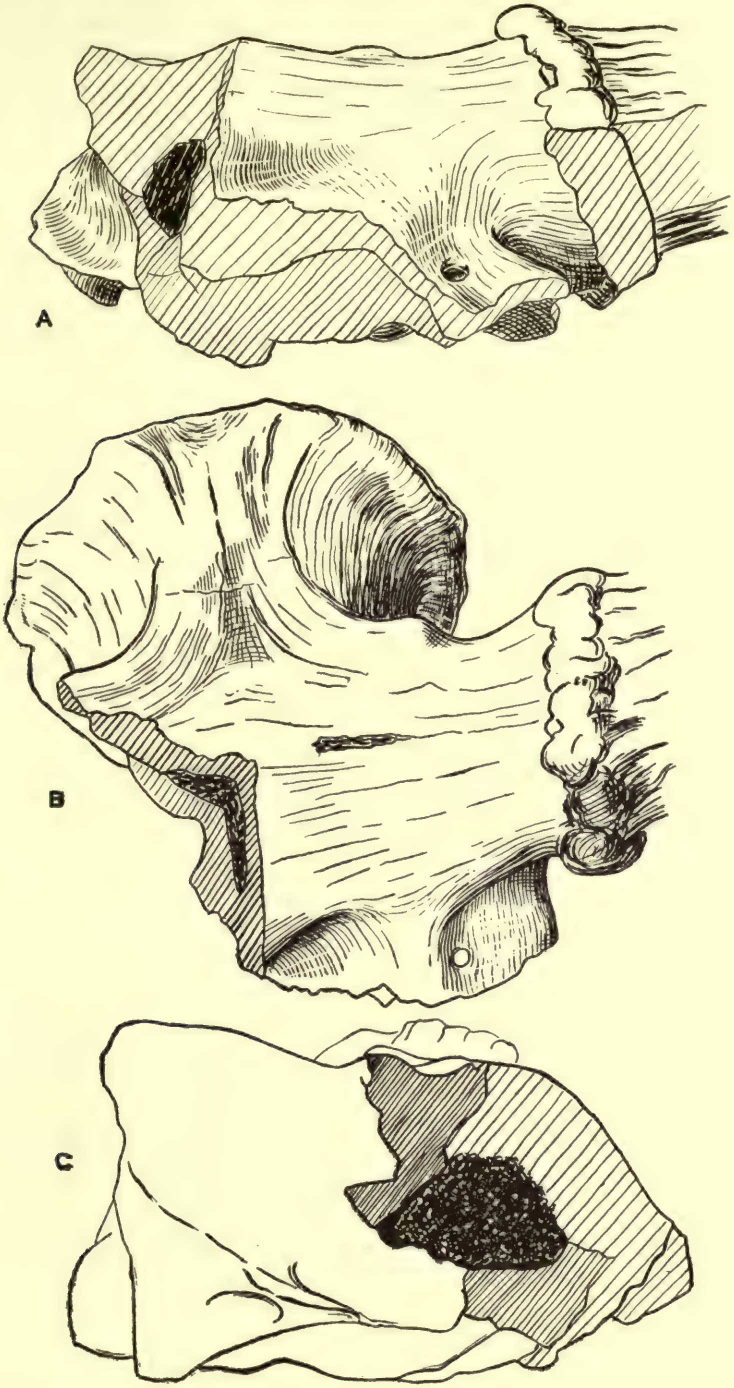

FIG. 6. *Libralces reynoldsi* holotype, Mundesley. B.M. (G.D.), M. 6553. A, front view ; B, upper view ; C, lateral view (the pedicle has been broken off and the anterior part of the brain cavity is exposed). ⅓ natural size. (Specimen figured by Reynolds, 1933, fig. 6*c*).

flattening of the palmation is distinctly felt at 25 cm. from the burr. The fragments from Sidestrand and from the Norfolk coast are nearly of the same size, but very incomplete. The smaller antler, from Trimingham (Gunn, 1891, pl. 5, fig. 4), has a diameter of 70 mm. above the burr, and shows that the more slender specimens tended to develop a long beam, as in *L. gallicus*: the flattening is not felt until 35–40 cm. from the burr.

The palmation is not preserved among the fossils of East Anglia, but fairly complete antlers, very probably of this species, have been found in Germany (see below). A maximal span of m. 2·50 has been recorded.

The identification of other specimens is made possible by their size.

It may be safely assumed that the muzzle of *Libralces* displayed the same positive allometry as the other ruminants. We can expect therefore that the difference in size between the teeth of *L. gallicus* and those of *L. reynoldsi* is greater than between their brain cases. No doubt such a comparison is valid only between broad limits, as it has to allow for individual and sexual variations, but it can be used here, where the species under consideration differ very greatly in size. Only two imperfect lower jaws, from Cromer and from Overstrand (Fig. 7), can be attributed to *L. reynoldsi*. Their size exceeds that of *L. gallicus* by roughly ½. The teeth are brachyodont, and display all the characteristic features of *Libralces*.

A humerus showing the characters of the *Alcinae* (Fig. 8), evidently belongs to this species. The proximal epiphysis and half of the distal epiphysis are missing, but from the remaining part a total length of 445–450 mm. can be inferred. A naviculocuboid (Fig. 8) and two phalanges may also be attributed to this species. The naviculocuboid is very large and massive, and relatively higher than the corresponding bone of the giant deer. The three cuneiforms are fused with it. The phalanges are long and slender as in *Alces*, but much larger.

OTHER LOCALITIES. Several remains from Eastern and Central Europe, attributed to *Alces latifrons* by authors, very probably have to be identified with *L. reynoldsi*. Pavlow (1906: 7, pl. 1, figs. 1, 2) described an incomplete antler and a lower jaw from Tiraspol (Bessarabia). The teeth, although much worn, show the same size and characters as those of *L. reynoldsi*. The antler is intermediate in size between the antlers from Mundesley and that from Trimingham, and its beam is relatively long; this seems to confirm the inference drawn from the English specimens that more slender individuals tend to develop longer beams. Another lower jaw with the same characters has been figured by Soergel (1923, pl. 2, figs. 5, 6). It was found in the sands at Mauer, together with other teeth and limb bones, among them a metatarsal of 450 mm. total length. This, too, fits very well with the size of the humerus from Overstrand. The same author stated (1913, 1923) that an "*Alces latifrons*" of nearly the same size is rather common at Mosbach, whereas at Süssenborn an "*Alces latifrons*" of a still larger size has been found. But it is hard to imagine how an animal of this structure could have developed a size still larger than that of our species. Possibly Soergel's statement was based on comparisons between the antlers. According to Vaufrey (1931: 538) more specimens of "*Alces latifrons*" have been found recently at Mosbach. The skull reproduced in his fig. 5, although too much reduced to permit exact comparisons, seems to belong

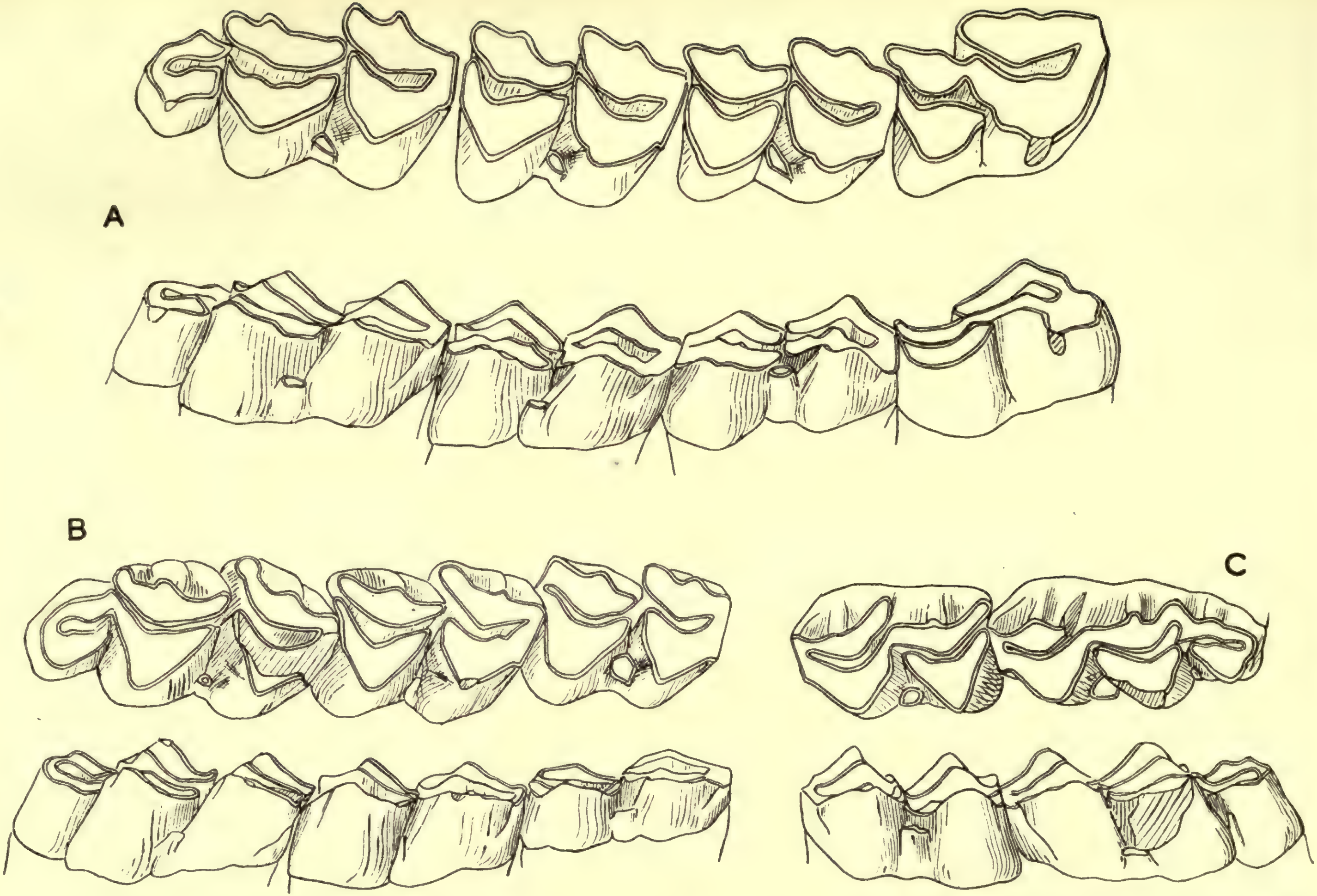

Fig. 7. A. *Libralces reynoldsi*, lower dentition, Cromer. Norwich Museum. 2.116.22. B. *L. cf. reynoldsi*, Lower molars, West Runton, Upper Freshwater Bed. B.M. (G.D.), Savin 1562. C. *L. reynoldsi*, lower molars, Overstrand. B.M. (G.D.), M. 6209. Natural size.

to *L. reynoldsi*. This author recorded a maximal span of m. 2·50 among the fossils from Mosbach.

Recently I have seen a fine lower jaw from Mosbach in the Museum of Natural History at Basel (D. 228), which in all its characters is identical with those of *L. reynoldsi* from the Forest Bed.

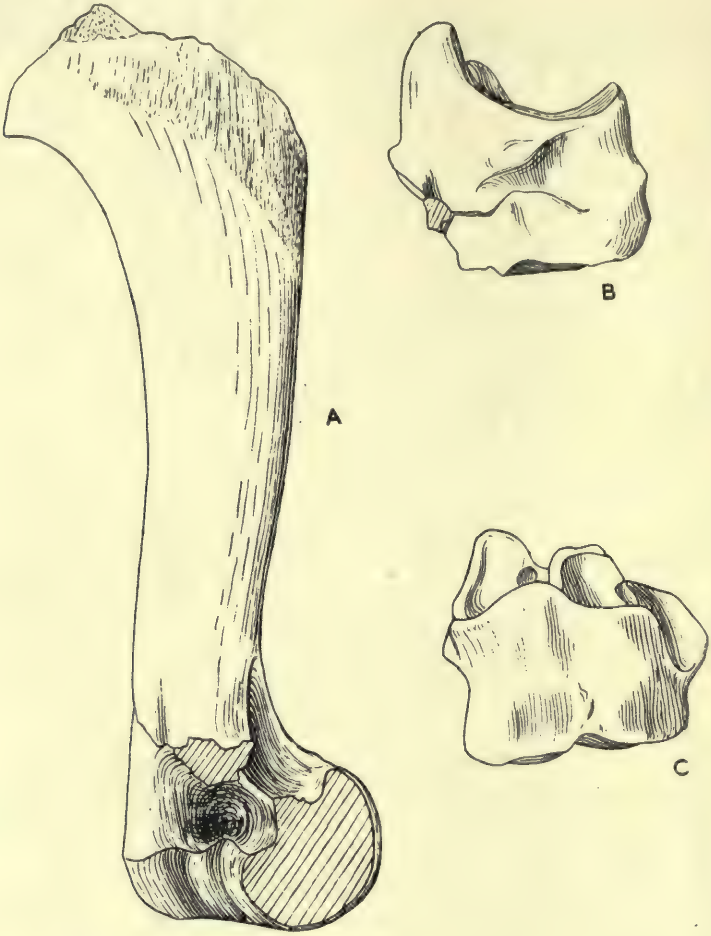

FIG. 8. A. *Libralces reynoldsi*, right humerus, Cromer. B.M. (G.D.), M. 6464. $\frac{1}{3}$ natural size. B & C. *L. reynoldsi*, left naviculocuboid, Overstrand. B.M. (G.D.), M. 6526. $\frac{4}{9}$ natural size.

THE RELATIONSHIPS OF *Libralces reynoldsi*. Although the record of *L. reynoldsi* is not fully satisfactory, its affinities with *L. gallicus* are clearly seen. It is highly probable that *L. reynoldsi* is its direct descendant. These two species differ mainly in size, and increase in size is a common evolutionary trend among ungulates. The antlers of *L. reynoldsi* seem to have evolved following a trend already hinted in

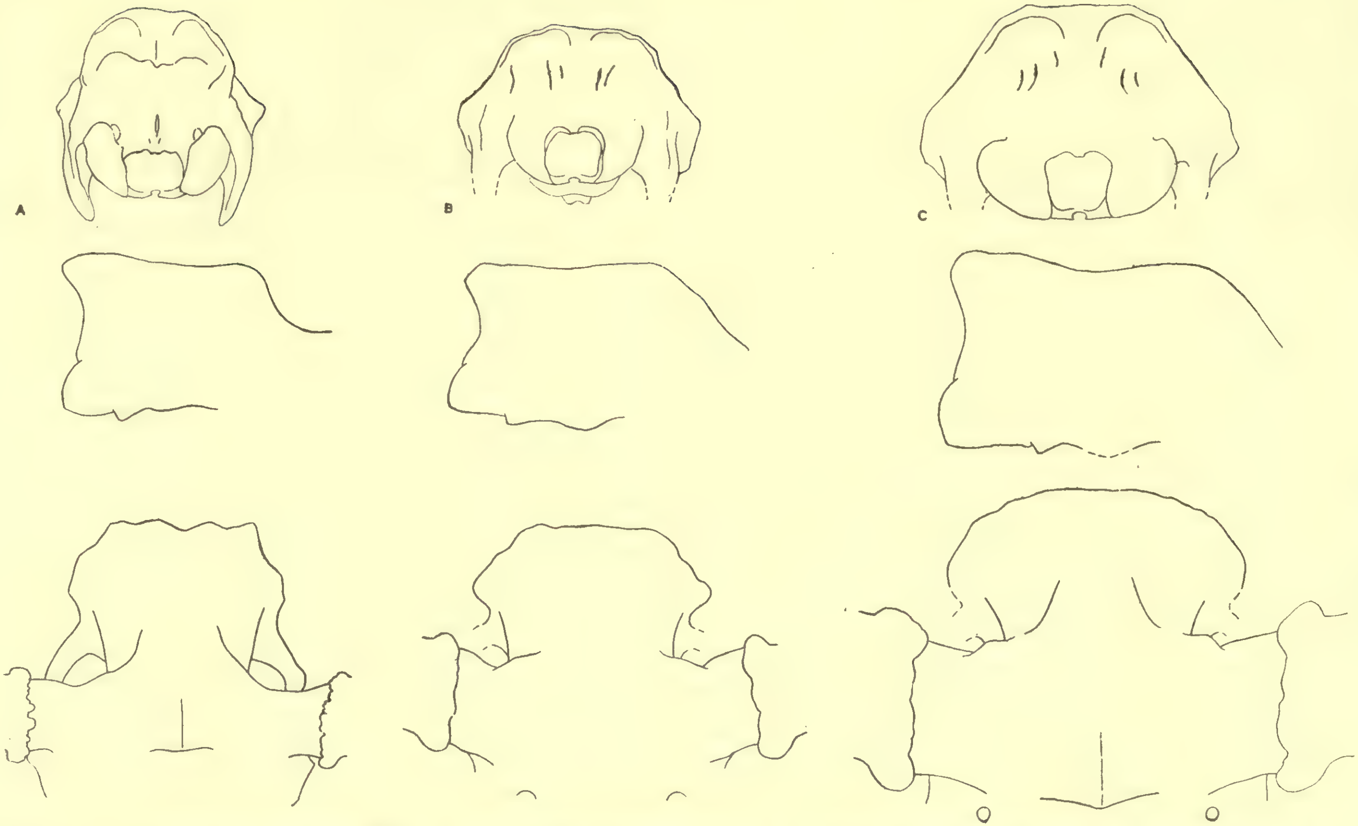

Fig. 9. Comparison of brain cases. A. *Alces alces*, male, Norway. B. *Libralces gallicus*, East Runton. B.M. (G.D.), M. 6101. Outline partly reconstructed. C. *L. reynoldsi*, holotype, Mundesley. B.M. (G.D.), M. 6553. Outline partly reconstructed. About $\frac{1}{5}$ natural size.

*L. gallicus*, that is, increase in size together with a shortening of the beam. Other differences in the skull, as shown above, are evidently correlated with the increase in weight of the antlers.

*L. reynoldsi* is distinctly larger than *Cervalces scotti*, and is the largest cervid so far known. It may be inferred that it stood m. 1·90 to m. 2·00 at the withers; its skull was very heavily built, but its limb bones were long and slender as in the other *Alcinae*.

MEASUREMENTS:—

Skull of the holotype:

| | |
|---|---|
| Occipital breadth | 218 |
| Occipital height | 135 |
| Minimal frontal breadth | 278 |
| Breadth of the brain case behind the pedicles | 171 |
| Breadth of the condyles | 132 |

Lower tooth row (Cromer, Norwich Museum. 2.116.22)

| | |
|---|---|
| Length of the three molars | 112 |
| Breadth of $M_2$ | 25 |

Humerus (Overstrand, B.M. (G.D.) M. 6462)

| | |
|---|---|
| Total length | 445–450 (inferred) |

First anterior phalanx (Mundesley, B.M. (G.D.) M. 6538)

| | |
|---|---|
| Total length | 100 |
| Proximal breadth | 42 |

First posterior phalanx (Trimingham, B.M. (G.D.) M. 6535)

| | |
|---|---|
| Total length | 101 |
| Proximal breadth | 38 |

Naviculocuboid (Overstrand, B.M. (G.D.) M. 6526)

| | |
|---|---|
| Antero-posterior diameter | 75 |
| Transverse diameter | 80 |
| Height | 42 |

## ***Libralces*** cf. ***reynoldsi***

From the Upper Freshwater Bed, West Runton.

(Fig. 7 B.)

A fragment of a lower jaw with the three molars, from the Upper Freshwater Bed at West Runton, is distinguished by the very poor development of the basal columns. The groove on the anterior crescent of $M_1$ is well marked; a shallow groove is present also on the anterior crescents of $M_2$ and $M_3$.

### ***Libralces minor*** n. sp.

(Figs. 4 A; 10 A, E, F.)

1934. *Alces latifrons* (Johnson): Reynolds (pars), fig. 6*a* ?, 7.

HOLOTYPE. A left lower jaw (B.M. (G.D.) M. 6227. No exact locality). Figs. 4 A, 10 A, 10 F.

ADDITIONAL SPECIMENS. Five incomplete lower jaws (one figured by Reynolds, fig. 7), and a lower molar, from East Runton and Sidestrand.

Possibly some fragments of antlers of a rather small size, from East Runton. The most complete of these fragments was figured by Reynolds, fig. 6*a*. Very doubtful specimens come from West Runton, Overstrand and Trimingham. (See also below.)

DIAGNOSIS. A *Libralces* with teeth smaller and distinctly narrower than those of *L. gallicus*.

DESCRIPTION. The teeth need no particular description. Apart from the smaller size and narrower form, they correspond in all respects to those of *L. gallicus*. The groove on the anterior crescent of $M_1$ is always clearly seen; it is not very clear in Reynold's photograph, which seems to have been retouched. A similar groove in $M_2$ is present in three specimens. The cross-section of the mandibular ramus is also distinctly narrower than in *L. gallicus* (Fig. 10).

The identification of the antlers is based on their size and is uncertain; it cannot be excluded that the specimens tentatively attributed to *L. gallicus* are young individuals of other species. The antler figured by Reynolds differs from those of *L. gallicus* in its smaller size, its much shorter beam and its relatively larger palmation. The other specimens from East Runton show the same characters but are still less complete. One of them (B.M. (G.D.) M. 6550), in Savin's opinion (note in the manuscript catalogue) is possibly the symmetrical part of Reynolds' specimen.

The fragments of beams from Overstrand, Trimingham and West Runton are very imperfect and much worn.

MEASUREMENTS:—

| | Holotype.<br>B.M. (G.D.) M. 6227 | East Runton.<br>B.M. (G.D.) M. 6210 |
|---|---|---|
| Lower tooth-row: | | |
| Total length . . . . . | 128 | 125 |
| Length of the three molars . . | 74 | 71 |
| Breadth of $M_2$ . . . . . | 14 | 15 |

### ***Libralces latifrons*** (Johnson)

(Figs. 10 B, C; 11)

1874. *Cervus latifrons* Johnson, pl. 1.
1887. *Alces latifrons* (Johnson) Dawkins (pars), pl. 1, fig. 6.

HOLOTYPE. A left antler from Happisburgh (Norwich Museum).

ADDITIONAL SPECIMENS. None surely identified, but possibly three lower jaws, from the Forest Bed of Mundesley (Figs. 10, 11), Walcott (Norwich Museum), and Cromer (private collection of J. E. Sainty). For more doubtful specimens see also later.

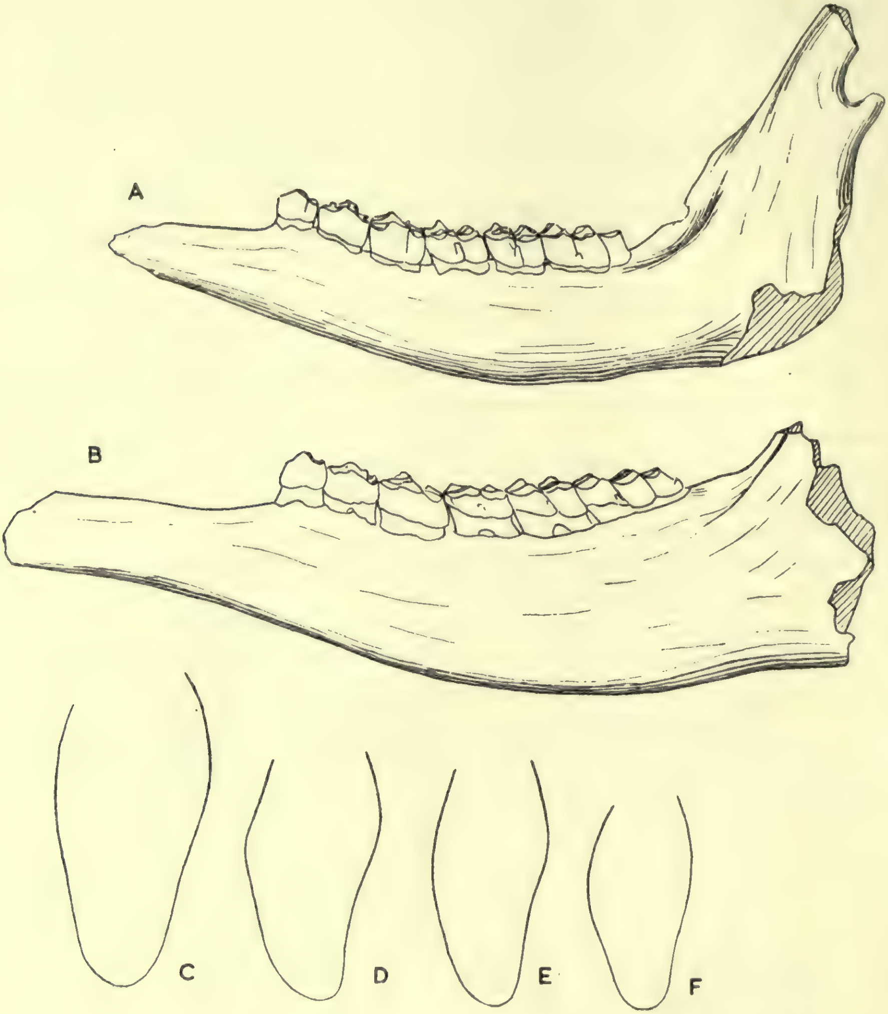

FIG. 10. A. *Libralces minor*, holotype. B.M. (G.D.), M. 6227. $\frac{1}{3}$ natural size. (See also Fig. 4.) B. *L. latifrons ?* Lower jaw from Mundesley. B.M. (G.D.), Savin 168. $\frac{1}{3}$ natural size. C–F. Cross-sections of lower jaws below the hinder lobus of M2. $\frac{2}{3}$ natural size. C. *L. latifrons ?* B.M. (G.D.), Savin 168. D. *L. gallicus*, East Runton. B.M. (G.D.), M. 6229. E. *L. minor*, East Runton. B.M. (G.D.), M. 6210. (Specimen figured also by Reynolds, 1933, fig. 7.) F. *L. minor*, holotype. B.M. (G.D.), M. 6227.

Description. This species is based on an incomplete left antler with a part of the frontal, and is ill defined. The pedicle is long and set horizontally, and the frontal is very thick, as in the other species of *Libralces*. The size is intermediate between those of *L. gallicus* and of *L. reynoldsi*. The antler differs from these species in having a short and straight beam; the palmation seems to have been very broad. The remaining portion of the frontal gives evidence of a larger animal than *L. gallicus*; on the other hand, the shortness of the beam makes it improbable that this fragment belonged to a young specimen of *L. reynoldsi*, but this evidence is by no means conclusive.

In the collections I have seen there are also three lower jaws of a size intermediate between that of *L. gallicus* and that of *L. reynoldsi*. *L. latifrons* is the only species with which I can tentatively identify them. The jaw from Mundesley (Figs. 10, 11) is fairly complete. Its cross-section is remarkably narrow and deep. There is a distinct burr behind the third lobe of $M_3$. A jaw from Walcott (Norwich Museum) and one found on the beach between Cromer and the Runtons (private collection of J. E. Sainty) are more imperfect.

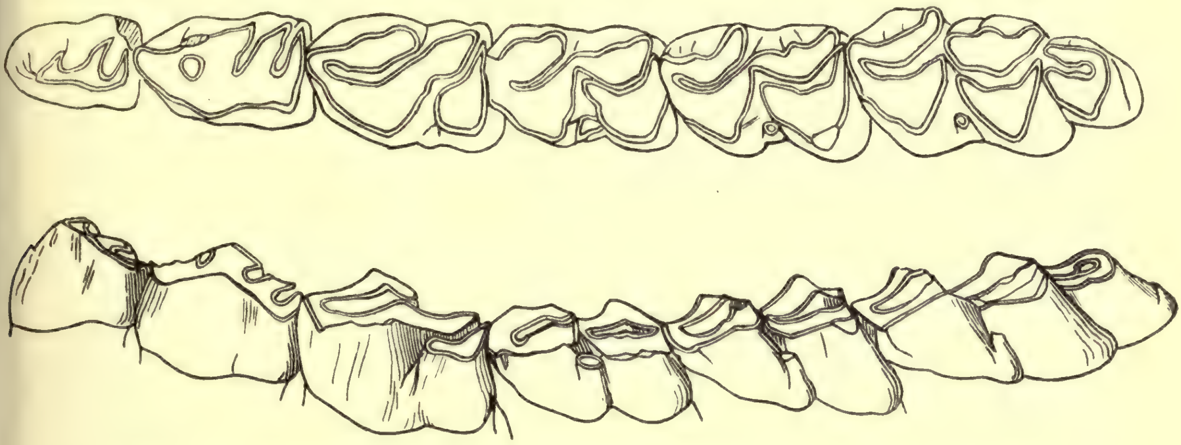

Fig. 11. *Libralces latifrons ?* Lower dentition, Mundesley. B.M. (G.D.), Savin 168. Natural size. (See also Fig. 10.)

Measurements:—

| | Mundesley. B.M. (G.D.) Savin 168 |
|---|---|
| Lower tooth-row : | |
| Total length . . . . . | 151 |
| Length of the three molars . . | 88 |
| Breadth of $M_2$ . . . . . | 20 |

### ***Libralces*** *incertae sedis*

(Figs. 12 A, B, C.)

As stated above, the distinction between the four species of *Libralces* is based mainly on the size. Many fragments therefore cannot be identified with certainty; in some instances it is practically impossible to distinguish the smaller species from young individuals of the larger species. A brief account of the most interesting fragments will be given here.

The fragments figured by Dawkins (1887, pl. 1, figs. 2, 3), both much worn, may possibly belong to *L. gallicus*. His pl. 1, fig. 4 is either *L. latifrons* or, more probably, *L. reynoldsi*. Gunn's type of *Alces bovides* (1891, pl. 1 A)may be either *L. gallicus* or *L. minor*. On his plate 5 Gunn figured many specimens attributed to *Alces bovides* and *Alces* sp. The specimen of fig. 5, much rolled, seems to belong to a small species; fig. 1 is the specimen figured by Dawkins on his pl. 1, fig. 2; fig. 2 is neither *Alces* nor *Libralces*; fig. 3 is *Libralces gallicus* (Dawkins' pl. 1, fig. 5), and fig. 4 is *L. reynoldsi* (see above).

The fragment figured by Reynolds, 1933, fig. 6*b*, is very doubtful, and might possibly belong to *Euctenoceros*.

Among the hitherto undescribed specimens, the following are the most interesting:

Fig. 12 A: A fragment of a frontal with the base of the antler, showing a very strong development of the burr. It belonged to a young specimen, probably *L. gallicus*. The frontal is rather thin (14 mm.).

Fig. 12 B: Another fragment of a frontal, with the base of the antler. The pedicle is very long and the flattening begins near to the burr. This is a young specimen of either *L. latifrons* or *L. reynoldsi*.

B.M. (G.D.) Savin 417.—A skull roof of a young specimen, very probably *L. reynoldsi*, from the Forest Bed at Sidestrand. The median suture is open and forms a median ridge. The supratemporal crests are well developed, the pedicles small, giving evidence that the antlers were not yet fully developed. In consequence, the frontal is very thin. Its thickness is 27 mm. on the median ridge, but on the sides of the ridge it is only 16 mm. and the thickness of the parietal is 11 mm.

Fig. 12 C.—An antler from the Forest Bed at Mundesley evidently belongs to an abnormal specimen. It bears a small anterior tine on its proximal portion and shows an abrupt bending at the middle. The characters of the surface sculpture, which shows very deep and large grooves, makes it probable that this fragment belongs to *Libralces*.

### Genus ***CAPREOLUS*** Hamilton Smith

There is not much to say about this genus. As far as I know, only *Capreolus capreolus* has been recorded from the Middle Pleistocene. According to Soergel (1923) this species is fairly common in Germany. The specimens from Mauer, which are of a larger size than the living species, have been distinguished by this author as *C. capreolus* mut. *prisca*.

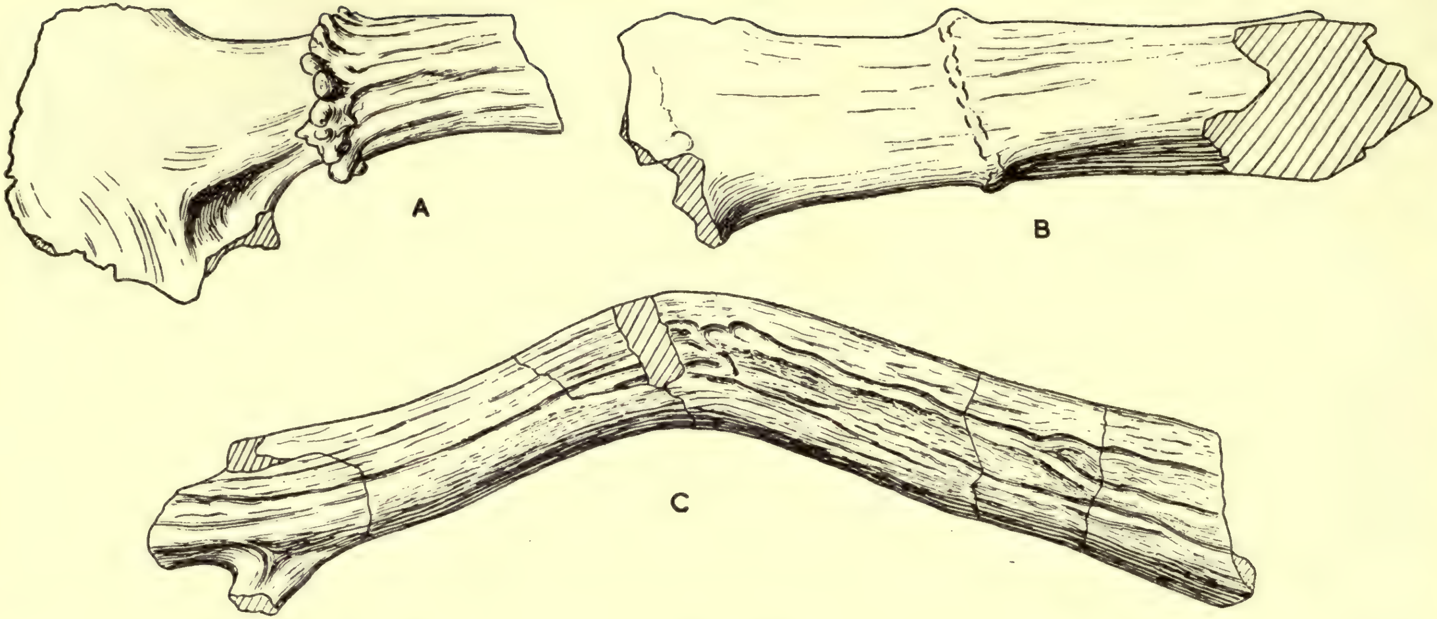

FIG. 12. A. *Libralces gallicus?* Young specimen, no locality. B.M. (G.D.), Savin 749. $\frac{3}{8}$ natural size. B. *L. reynoldsi?* Young specimen from Bacton. B.M. (G.D.), Savin 239. $\frac{3}{8}$ natural size. C. *L. gallicus?* Abnormal specimen from Mundesley. B.M. (G.D.), Savin 196. $\frac{1}{4}$ natural size.

### *Capreolus capreolus* (L.)

1882. *Cervus capreolus* L.: Newton, p. 52.
1933. *Cervus capreolus* L. (= *Capreolus caprea* Gray): Reynolds, p. 34, fig. 15.

Distribution. Forest Bed at Overstrand, Ostend, Sidestrand. Doubtful at Happisburgh and Cromer. Upper Freshwater Bed at West Runton.

Newton (1882) questioned the occurrence of the roe in the Forest Bed series. In his opinion a fine antler from Happisburgh (Geol. Survey) may have been found either in the Forest Bed or in the overlying postglacial drift, whereas another specimen from Cromer (Baker coll.) is also of doubtful origin. But Reynolds recorded this species from the Forest Bed of Bacton, Ostend, Overstrand and West Runton (U. Freshwater Bed ?), and figured three fine antlers. In the Savin collection there are in addition a lower jaw from the Forest Bed of Sidestrand and several fragments from the Upper Freshwater Bed of West Runton, namely, two young antlers, three incomplete lower jaws and several isolated incisors and upper molars. There is no reason therefore to question its occurrence in the Forest Bed and Upper Freshwater Bed. The size is somewhat variable, but the material is too scanty for good comparisons.

### Genus ***CERVUS*** L.

The classification of the many species and subspecies of this genus is a thorny problem to palaeontologists. In the very abundant literature many names have been proposed, but the value of a great part of them is questionable. The distinctions have generally been based on antler characters, which may be deceptive owing to the wide range of individual variation. However, they still give the most useful data. The remains of the skull are largely represented by the less significant parts, namely brain cases, lower jaws and teeth. Moreover comparisons with the living species and races are made difficult by the fact that zoologists base their classification mostly on external characters, generally giving little attention to the skulls. However, Pocock's recent studies (1942–43*a*) on the Indian deer have shown that skulls also may eventually afford valuable data.

A fairly complete account of the species and subspecies of this genus has been given by Lydekker (1915: 116 ff.). He distinguished in the genus *Cervus* seven species; on one of these, *C. albirostris*, Flerow (1930) has founded the genus *Przewalskium*. The remaining six species are: *C. elaphus* L., *C. canadensis* Erxl., *C. yarkandensis* Blanford, *C. wallichi* Cuvier, *C. macneilli* Lydekker, *C. cashmirianus* Gray; the last falls under the synonymy of *C. hanglu* Wagner. They are all characterized by the presence of a bez tine.

*C. canadensis*, the wapiti, with many varieties ranging from N. America to Central Asia, and *C. macneilli*, ranging over Szechuan, Kansu and Yunnan, are distinguished by the upper tines being placed in a plane parallel to the median plane of the head.

In the other species the upper bifurcations take place transversally to the median plane. *C. wallichi* and its variety *C. wallichi affinis*, the shou (Sikkim and Tibet), are of a very large size. The antlers have generally five tines and end with a simple transversal fork. An accessory tine seems to occur very rarely. This species has been redescribed recently by Pocock (1942–43*a*), who gave the two varieties full specific rank. *Cervus hanglu*, the hangul, from Kashmir, is a little smaller than *C. wallichi*. Its antlers are similarly built, but an accessory tine or even a double terminal fork are not uncommon (see the good photograph by Stockley, 1948). This species also has been redescribed by Pocock (1942–43*a*). *C. yarkandensis*, from E. Turkestan, has antlers of the same type, generally with five tines, eventually with an accessory tine.

*C. elaphus*, the familiar red deer, is distinguished by a greater complication of the antlers. As a rule they end with four or more tines forming the characteristic "cup" ("Krone" of the German authors), originated by the fusion of two or more transversal forks (Beninde, 1940). The cup is very variable, especially in some living stocks, which in many ways are influenced by unnatural conditions of life. This, however, does not alter the fundamental fact that the cup is a peculiar feature of *Cervus elaphus*. In the Upper Pleistocene European red deer it is fairly constant.

This species has given origin to many varieties or geographical races; the eastern races are generally larger, but do not attain the size of the wapiti. In the smaller races the antlers are less complicated and the bez tine is sometimes lacking, but the cup, as a rule, is still present.

The typical area of the species is Southern Sweden. Lydekker (1915) listed the following subspecies: *C. elaphus barbarus* Bennett, Algeria and Tunisia; *C. elaphus corsicanus* Erxl., Corsica and Sardinia; *C. elaphus hispanicus* Hilzheimer, S.W. Spain; *C. elaphus atlanticus* Lönnberg, Trondhjem district, Norway; *C. elaphus scoticus* Lönnberg, Scotland; *C. elaphus hippelaphus* Kerr, Germany; *C. elaphus*, unnamed subspecies, Bukovina; *C. elaphus maral* Ogilby, Caucasus and Persia. To these we may add *C. elaphus bolivari* Cabrera, Central and Northern Spain; *C. elaphus brauneri* Charlemagne, Crimea.

The value of some of these subspecies, even as geographical races, is questionable. The craniological studies by Ingebrigtsen (1922–23, 1927) are instructive. According to this author, no distinction is possible between the red deer of Sweden, Germany and the Norwegian mainland districts. Some stocks of the Norwegian isles, especially from Hitra, have developed a smaller size, which is due only to environmental factors and is no expression of hereditary differences. This is true also for the Scottish red deer (see also Ritchie, 1920), and is possibly true for *C. elaphus corsicanus* and *C. elaphus hispanicus*. But two subspecies at least seem to be genetically established: the small *C. elaphus barbarus*, distinguished by its spotted pelage, and the large *C. elaphus maral*, with large but relatively simple antlers and cruciform nasals; this character, as far as I know, has not been recorded in the literature, but is well developed in all the skulls of Caucasian stags exhibited in the British Museum.

No attempt at a complete revision of the fossil red deer will be made here, but it may be useful to give a short account of its earlier representatives.

The red deer has no relatives in the Villafranchian faunas of Central and Western Europe. Redstone (1930) quoted it from the Red Crag, but Dr. K. P. Oakley informs me that the specimen referred to actually came from overlying late Pleistocene deposits. The red deer immigrated from Eastern Europe or from Asia during the Mindel-Riss interglacial, and possibly other immigrations took place later. The best known representatives of the oldest European red deer are not identical with living red deer, and there is no proof of the occurrence of the typical form of *Cervus elaphus* in the Mindel-Riss interglacial.

The most perfect representatives of the genus *Cervus* s. str. were found at Mosbach and Mauer and have been described by Beninde (1937). Further details were added by Haupt (1938), Kleinschmidt (1938) and Schmidtgen (1938).

*Cervus acoronatus* Beninde, from the sands of Mosbach (main fauna), is a species of large size. It has stout and massive antlers, with five tines, namely, well developed brow and bez tines, a trez tine and a flattened terminal fork, set transversally to the axis of the body. Schmidtgen (1938) has figured an unusually flattened terminal fork, and Kleinschmidt (1938) a terminal fork with a small accessory tine. As a whole, *C. acoronatus* seems to constitute a rather uniform and well characterized stock. The lack of the cup led Beninde to distinguish it from *Cervus elaphus* as a full species. The antlers strikingly recall those of the red deer of Central Asia, especially of the large *C. wallichi*, from which they seem to differ only by the marked flattening of the upper fork and by a stouter form.

Haupt (1938 : 32) proposed to change the name *C. acoronatus* into *C. elaphus mosbachensis*, but this is obviously contrary to the rules of nomenclature. According to Beninde, imperfect antlers of a smaller size occur in the same sands. It is not clear whether they belong to young individuals or to a distinct species.

The deer from Mauer, of nearly the same age if not a little younger, is more poorly represented; it has no typical cup and closely resembles *C. acoronatus*, from which it is distinguished by a twisting of the upper fork, bringing its anterior surface obliquely outwards, and by the presence on it of accessory tines, eventually lying out of its main plane.

Soergel (1923) gave this species the name *C. elaphus* mut. *prisca*, changed into *C. elaphus priscus* by Beninde, but this name is preoccupied. Kleinschmidt (1938*a*) proposed the name *C. benindei*, and in the same year Haupt proposed *C. elaphus mauerensis*. *C. benindei* has the priority, as it was published in the first months of 1938 (the fascicle was purchased by the British Museum in March), whereas Haupt's paper was published in the second half of the year (see on p. 3 of the same volume the necrology of G. Klemm, who died on 6th August, 1938).

This form is more closely related to *C. acoronatus* than to later red deer; there is no reason therefore to rank it as a subspecies of *C. elaphus* Here it will be called *C. benindei*.

In 1937 Beninde supposed that the upper fork of the red deer from Mauer might represent an intermediate stage, leading to the formation of the cup. This however is not in accordance with his later conclusions (1940) on the origin of the cup, based on comparative studies of recent red deer, that is, that the cup originated through the fusion of two or more transversal forks. The peculiar position of the terminal fork of *C. benindei* does not occur in later red deer. Beninde himself seems to have changed his mind, as he wrote (1940 : 256) : " Im I Interglazial des Oberrheins (Mosbach, Mauer) liegen Geweihe, die gegen den heutigen Rothirsch eine ganz eigene Stellung einnehmen. Aber bereits um das Riss (Steinheim a.d. Murr, Primigenius-horizont) erscheinen Hirsche vom rezenten Typus . . . "

The validity of *C. acoronatus* and *C. benindei* has been questioned by Bachofen Echt (1941), who claimed to see intermediate stages between these two species and *C. elaphus* among the fossils from Hundsheim. However, his observations, which are based on two imperfect specimens, do not invalidate Beninde's conclusions. Moreover the age of Hundsheim, according to Kormos (1937) is " . . . vielleicht etwas jünger als das Upper Freshwater Bed von West Runton." If so, it is younger than the main faunas of Mosbach and Mauer.

The remains from the other localities of the same age are scanty and imperfect. They are not identical with the species of Mosbach and Mauer, but do not demonstrate the presence of the true *Cervus elaphus* in the second Interglacial. The denomination *Cervus* cf. *elaphus* better expresses our state of knowledge.

The red deer from Süssenborn, to which Pohlig (1909) gave the name *C. elaphus trogontherii*, is rather large, and seems to be characterized by the lack of the bez tine. The status of the red deer in this locality is however not clear. Some years later Soergel (1923 : 221) quoted *Cervus elaphus* cf. mut. *prisca* Soerg., *Cervus maral fossilis* Ogilby (*sic*), *Cervus* (*Elaphus* n. sp., grosse Form).

A basal portion of an antler from Tiraspol (Pavlow, 1906, pl. 1, fig. 8) is large and stout and bears a strong bez tine.

The red deer from the Upper Valdarno (Azzaroli, 1948) also belongs to this period. It is of a medium size and its antlers are poorly known.

Stehlin (1932) made reference to other early red deer from Jockgrim, Bammental, St. Prest and Solilhac. The faunas of Solilhac however are not older than the Riss glaciation (Bout & Cailleux, 1951).

The true *Cervus elaphus* is certainly present in the Riss glaciation. Good specimens from the *Antiquus*-horizon of Steinheim a.d. Murr have been distinguished by Beninde (1937) under the subspecies *C. elaphus angulatus*. The red deer of the overlying *Primigenius*-horizon is not distinguishable from the typical form.

### ***Cervus* cf. *elaphus* L.**

(Figs. 13, 14.)

1882. *Cervus elaphus* ? L. : Newton, p. 55.
1891. *Cervus elaphus* L. : Newton, p. 27, pl. 4, fig. 14.
1931. *Cervus elaphus* L. : Reynolds, p. 4.

OCCURRENCE. This is a very common species in the Forest Bed and in the Upper Freshwater Bed, but its remains are rather poor. In 1882 Newton questioned the occurrence of the red deer in the Forest Bed, but included it in his faunal list in 1891. He pointed out that it was then the earliest record of the red deer. Reynolds recorded it from the Forest Bed at Happisburgh, Overstrand, East Runton and Trimingham. The specimens I have seen bear the indications : Trimingham, Sidestrand, Bacton, Overstrand, Happisburgh, Mundesley, East Runton (one specimen, much rolled), West Runton (Upper Freshwater Bed), Palling (on the beach).

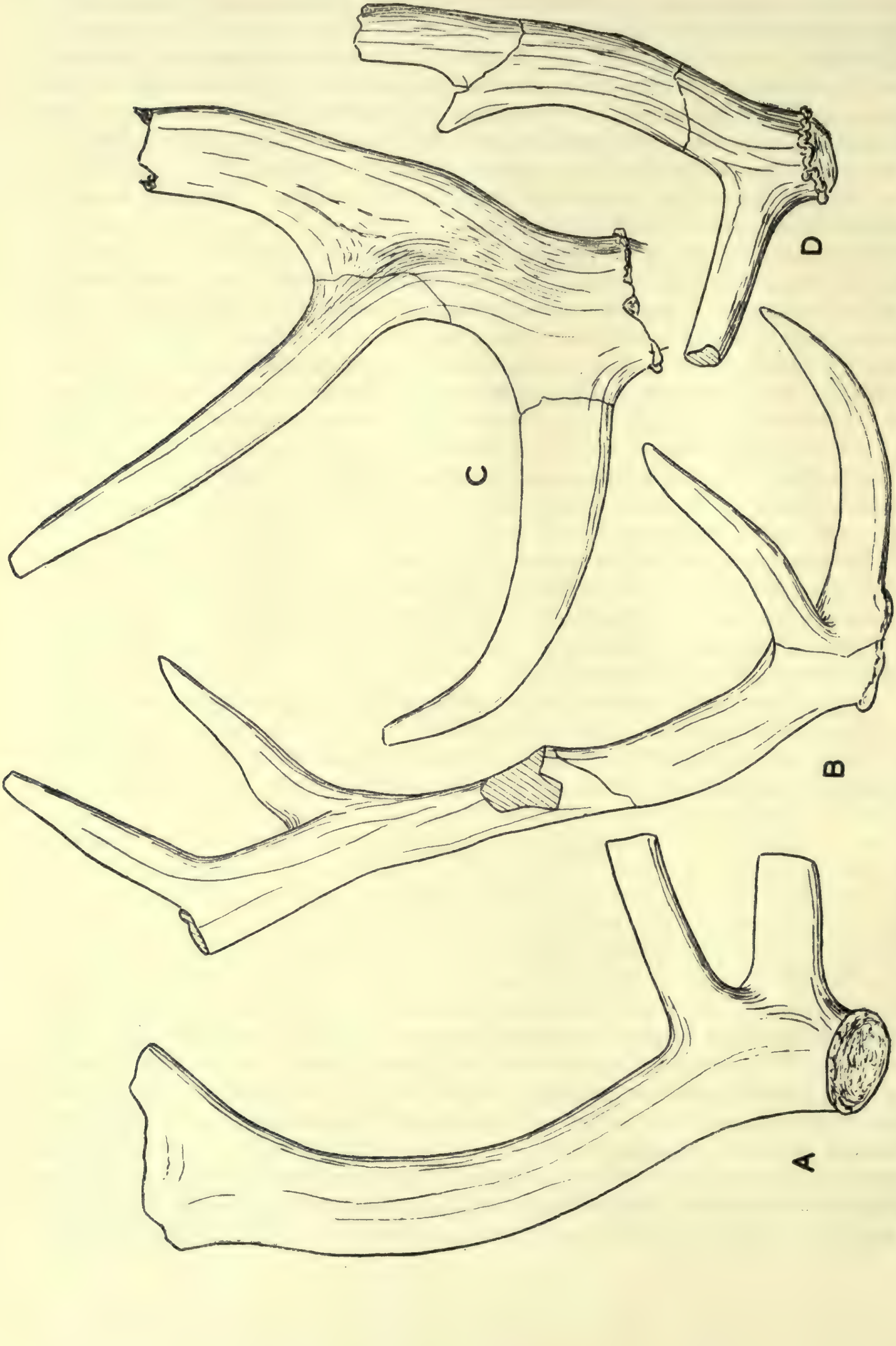

Fig. 13. *Cervus* cf. *elaphus*. Antlers, ¼ natural size. A. Bacton, B.M. (G.D.), Savin 297. B. Trimingham, B.M. (G.D.), Savin 1037. C. Trimingham, B.M. (G.D.), Savin 1349. D. Trimingham, B.M. (G.D.), Savin 1418.

Description. The antlers consist for the most part of basal fragments, and differ greatly in size; some of them are very massive (Fig. 13). The bez tine is generally well developed, and in some instances is pushed upwards. In one young specimen it does not occur in its typical form, but we find here a small tine which may be interpreted indifferently as a bez or a trez (Fig. 13 D). Possibly however some fragments of this species without a bez have escaped my attention.

The only fairly complete antler is of medium size and is very stout. Its upper portion ends with three tines originating from two successive bifurcations, and is damaged. This antler cannot be identified with the species of Mauer and Mosbach, but does not show the typical cup of *C. elaphus*. As it seems to belong to a not fully grown specimen the question of its identity is still open.

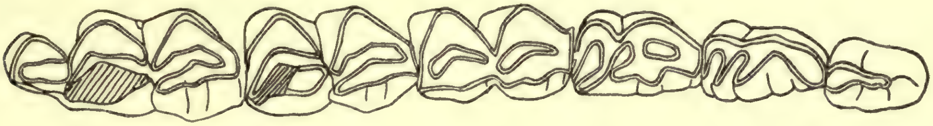

Fig. 14. *Cervus* cf. *elaphus*, lower dentition, Trimingham. B.M. (G.D.), M. 6220. Natural size.

Four lower jaws, from Trimingham and from the Upper Freshwater Bed at W. Runton, do not show any remarkable feature. $P_4$ is always advanced.

The attribution of some limb bones will be discussed later.

### Genus ***EUCTENOCEROS*** Trouessart

A definition of this genus and a discussion of its synonymy have been given in previous papers (Azzaroli, 1948; Bout & Azzaroli, 1953). In these papers I did not include in it "*Cervus*" *falconeri* Dawk., whose relationships were not clear to me. Kunst (1937) pointed out its affinities to *E. teguliensis* (= *E. ctenoides*; see below), but as a matter of fact these two species differ in many characters. On the contrary its affinities with *E. sedgwicki* are very close. I therefore include it in this genus. It is the oldest and most primitive of its species, but not their common ancestor.

Unfortunately in 1948 I overlooked Nesti's description of the species from the Upper Valdarno, which is not quoted in Forsyth Major's papers and is recorded only in Sherborn's catalogue. Nesti exhibited the deer from the Upper Valdarno at a congress of Italian scientists held in Florence in 1841, and proposed for the larger species the names *Cervus dicranios*, *Cervus ctenoides* and *Cervus orticeros*. His verbal description was summarized in the report of the meeting by the secretaries, Savi & Sismonda (1841). The name *Cervus orticeros* has been subsequently ignored and is probably synonymous with *C. ctenoides*.

These two species have been briefly described also by Cornalia (1858–71: 61). The incorrect spelling *dicranius* has been introduced by Forsyth Major.

The species of this genus display very peculiar features in the antlers, which make them easily distinguishable from other genera. The first tine branches from the outer anterior part of the beam; the following tines arise from its anterior part and lie in a plane. They are numerous, three in *E. falconeri*, four or five in the other species, and are frequently more or less undulated. Beam and tines display a tendency to become flattened and in some species the tines subdivide further. The flattening is generally more pronounced in the upper portion of the antlers, but in *E. sedgwicki* reaches as far down as the brow tine. In the larger specimens of some species a small accessory tine, directed upwards, is given off from the first bifurcation.

With the sole exception of *E. falconeri* all the species of this genus are of a large size. Together with the common features described above, they display a remarkably wide range of variation which makes specific distinctions difficult. I do not feel satisfied with some of the determinations I published in 1948. An antler from Olivola (fig. 8) then attributed to *E. ctenoides* is actually of *E. dicranios*. The tines of this specimen do not show the strong backward bending of the lectotype, but in its general characters this antler is more similar to it than to *E. ctenoides*. Moreover, my reconstruction was wrong: the lower tine preserved in this antler corresponds to the second tine, not to the third tine of the lectotype of *E. dicranios*.

*E. ctenoides* and *E. teguliensis* are very probably identical. The antlers do not afford any good basis for distinction.

### ***Euctenoceros tetraceros*** (Dawkins)

(Figs. 15, 16, 17 A, B, D.)

1878. *Cervus tetraceros* Dawkins, p. 416, figs. 14, 17.
1891. " *Cervus tetraceros* Mackie " : Newton, p. 32, pl. 4, fig. 2.
1953. *Euctenoceros tetraceros* (Dawk.) : Azzaroli *in* Bout & Azzaroli, p. 43, figs. 1–6.

OCCURRENCE. Fairly common at East Runton, rare at Overstrand.

DESCRIPTION. This species is represented by two fine antlers (Fig. 15) and several fragments. They all agree with the specimens from Peyrolles; one specimen only (Fig. 16) is distinguished by the abnormal inward bending of its brow tine. As at Peyrolles, all the antlers of this species have been naturally shed.

Three lower jaws show the same characters as those from Peyrolles. Probably also a fourth lower jaw with a primitive $P_4$ belongs to this species.

MEASUREMENTS:—

| Lower tooth rows: | East Runton. B.M. (G.D.) M. 6232 | East Runton. B.M. (G.D.) M. 6218 | East Runton. B.M. (G.D.) M. 6221 |
|---|---|---|---|
| Total length | 131 | 134 | 133 |
| Breadth of $M_2$ | 16 | 15 | 15 |

### ***Euctenoceros ctenoides*** (Nesti)

1841. *Cervus ctenoides* Nesti (in Savi & Sismonda, p. 159).
1858–71. *Cervus ctenoides* Nesti : Cornalia, p. 61.

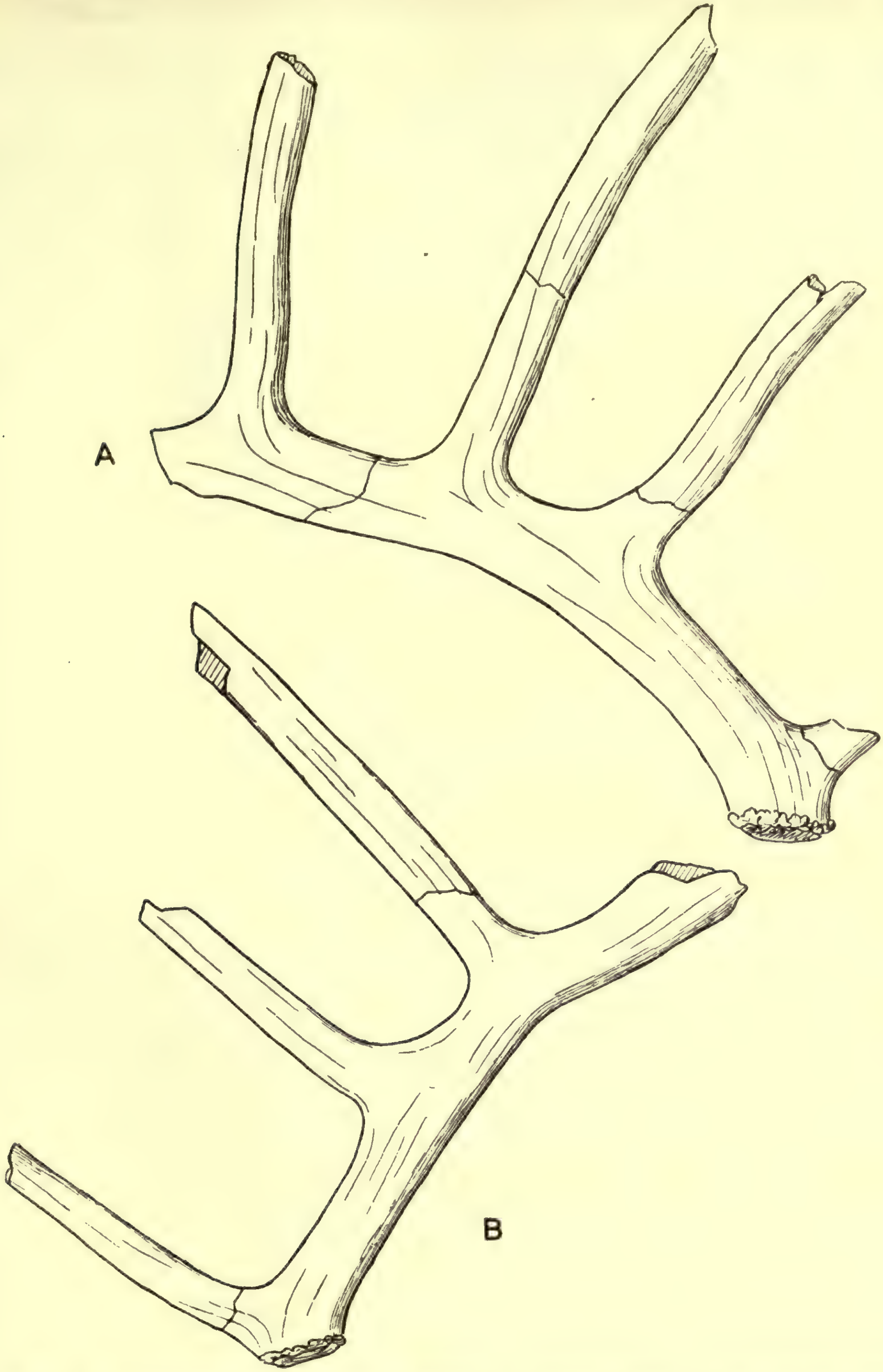

FIG. 15. *Euctenoceros tetraceros,* East Runton. ¼ natural size. A. Left antler, B.M. (G.D.), M. 6369. B. Right antler, B.M. (G.D.), M. 6370.

1887. *Cervus savini* Dawkins (pars), pl. 3, fig. 4.
1948. *Cervus* (*Euctenoceros*) *ctenoides* Nesti : Azzaroli (pars), p. 62, figs. 6, 7, 9.
1947. *Eucladoceros teguliensis* Dub. : Hooijer, p. 34 (cum syn.).

SYNONYMY. The distinction between *E. ctenoides* and *E. teguliensis* does not seem to be valid. The ranges of variation of these two species widely overlap. The antlers from Tegelen do not attain the size of the larger specimens from the Upper Valdarno, but this may be due merely to the incompleteness of the record. The dentition and limb bones are of the same size.

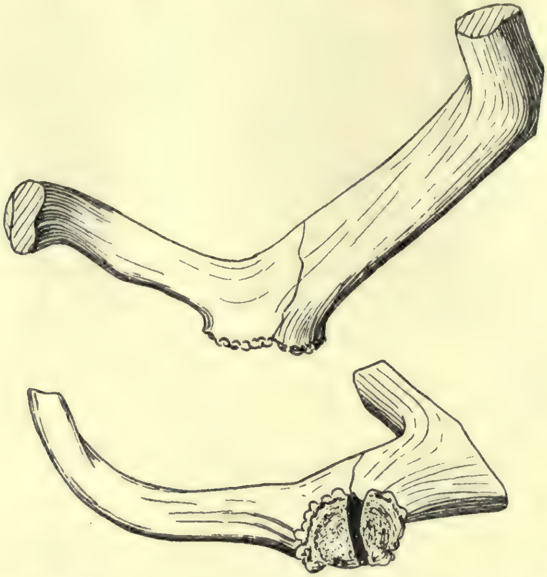

FIG. 16. *Euctenoceros tetraceros*, abnormal right antler, East Runton. B.M. (G.D.), M. 6399. ¼ natural size.

Among the specimens from East Anglia a very fine antler from Sidestrand (Dawkins' pl. 3, fig. 4) so closely resembles the lectotype of *E. ctenoides* that no one would hesitate to identify it with this species.

OCCURRENCE. The only good evidence of the occurrence of this species is given by the antler from Sidestrand figured by Dawkins, who incorrectly attributed it to *Cervus savini*, and by some basal fragments from East Runton, of a slightly smaller size.

For the identification of other fragments of antlers and of dentitions see later.

### ***Euctenoceros sedgwicki*** (Falconer)

(Figs. 18, 19, 20 A, 21 A, F.)

1868. *Cervus sedgwicki* Falconer (*ex* Gunn MSS.), p. 472, pl. 37, figs. 1–3.
1882. *Cervus sedgwicki* Falc. : Newton, p. 60.
1891. *Cervus sedgwicki* Falc. : Gunn, pl. 3, figs. 99, 100.
1891. *Cervus* sp. Gunn, pl. 3, figs. 105, 106.
1891. *Cervus sedgwicki* Falconer : Newton, p. 31.

Occurrence. This species is fairly common, but is represented for the most part by very imperfect fragments. The only satisfactory specimen is the holotype (Fig. 18). This and most of the other fragments were found at Bacton, a few specimens at Mundesley and a much rolled fragment at East Runton. For doubtful fragments see also below.

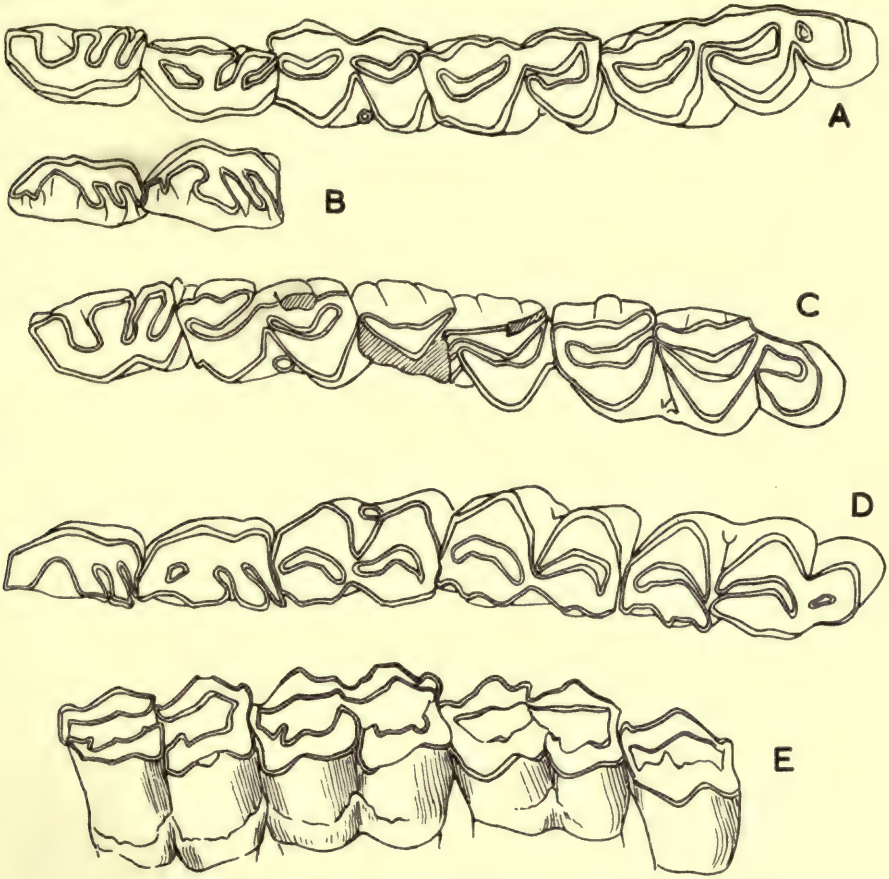

Fig. 17. *Euctenoceros;* dentition, East Runton. Natural size. A. *E. tetraceros*, B.M. (G.D.), M. 6218 (advanced form). B. *E. tetraceros*, B.M. (G.D.), M. 6221 (primitive form). C. *E. ctenoides ?* B.M. (G.D.), M. 6241 (primitive form). D. *E. tetraceros*, B.M. (G.D.), M. 6206 (advanced form). E. *E. ctenoides ?* B.M. (G.D.), M. 6213.

Description. This species is of a large size and is characterized by the high position of the brow tine, 10–15 cm. above the burr, and by a very marked flattening of the upper portion of the beam and of the tines, which divide into three or four secondary tines. The brow tine is also much flattened, and in the type it divides into four points. The high position and the flattening of the brow tine are remarkably constant, and are well displayed even in young specimens (Fig. 21 F). The pedicles are set near one another, as in *E. boulei* and *E. dicranios*.

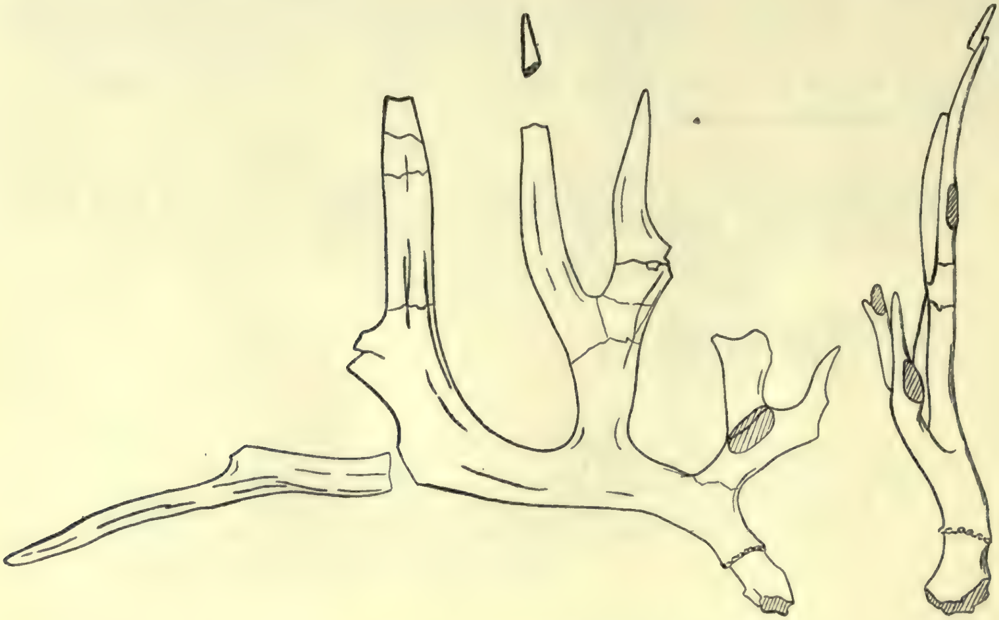

FIG. 18.—*Euctenoceros sedgwicki*, holotype, Norwich Museum, Gunn Colln. No. 99. $\frac{1}{13}$ natural size.

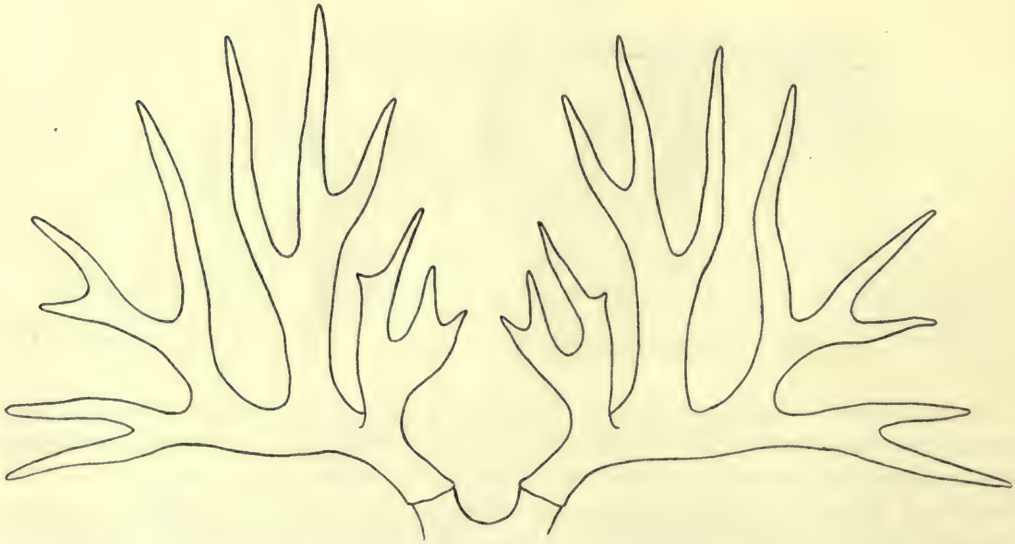

FIG. 19. *Euctenoceros sedgwicki*, reconstruction of the holotype. Norwich Museum, Gunn Colln. No. 99. $\frac{1}{8}$ natural size.

The upper portion of the type antler is badly damaged and its reconstruction is rather puzzling. On Fig. 18 I have indicated the most probable position of the fragments. The small cross-section of the beam at the broken surface makes it unlikely that there were additional tines. On Fig. 19 I have attempted a reconstruction of this specimen.

COMPARISONS. *Euctenoceros falconeri* (Dawkins, 1868; see also Kunst, 1937: 101) is a species of medium size. It does not occur in the Weybourn Crag nor in the Forest Bed, but has been found in the Red Crag and in the Norwich Crag.

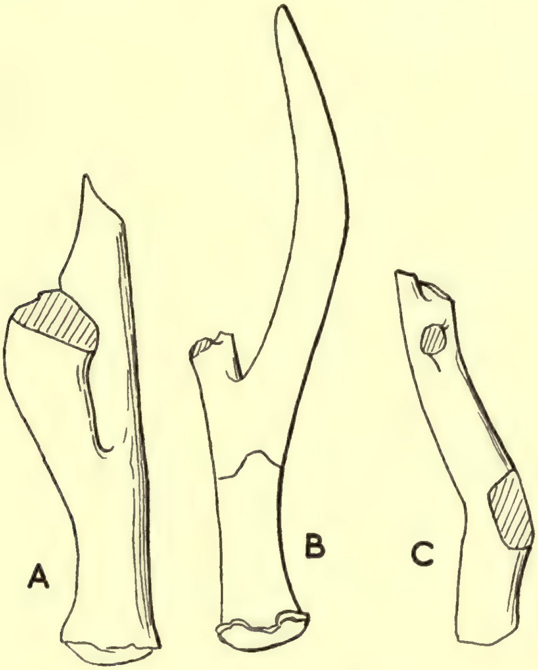

FIG. 20. *Euctenoceros sedgwicki* and *E. falconeri*, lower portions of the antlers. ⅛ natural size. A. *E. sedgwicki*, Mundesley. Norwich Museum 323. B. *E. falconeri*, Thorpe, Norwich Crag. Norwich Museum 313. C. *E. falconeri*, Horstead, Norwich Crag. Norwich Museum 310.

It occurs also in the Poederlian of the Netherlands and in deposits of the same age in Belgium. The most complete specimens were found in the Belgian Kempen. The remains from East Anglia are rather fragmentary; the most complete are the holotype (a young individual), and a crushed full-grown antler from the Red Crag, now in the Museum at Ipswich. In the British Museum and at Norwich I have seen other fragments from the Norwich Crag, and at Ipswich fragments from the Red Crag. The remains of the Norwich Crag may possibly have been derived from the Red Crag. Those from the Red Crag bear no exact indication of the horizon, but their state of fossilization shows that they were not derived.

Two specimens in the Norwich Museum were figured by Gunn (1891, pl. 2, fig.

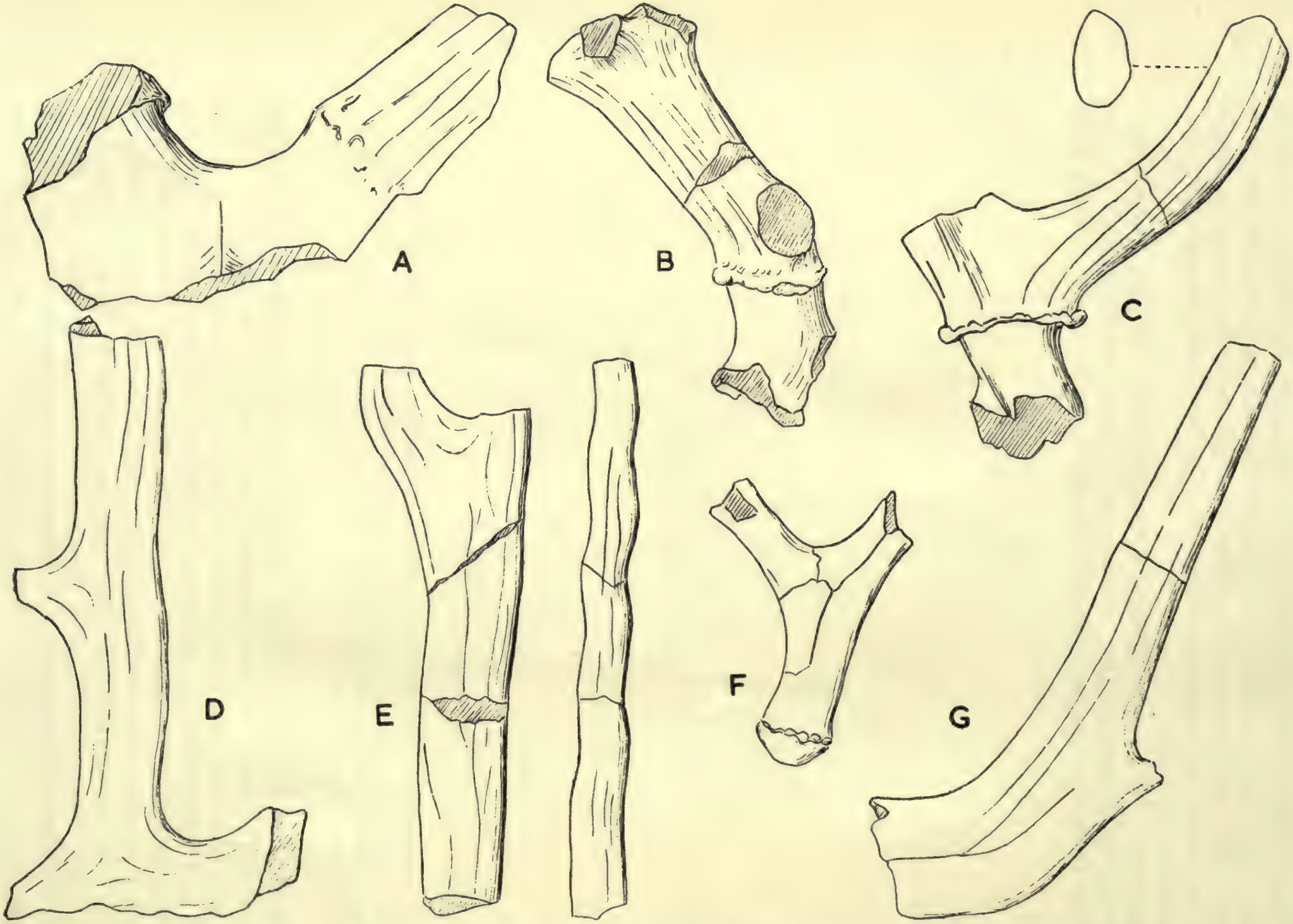

FIG. 21. *Euctenoceros*, fragments of antlers. A. *E. sedgwicki*, frontal and base of an antler from Bacton. B.M. (G.D.), Savin 244. $\frac{1}{3}$ natural size. B. *E. ctenoides ?* Right antler, with abnormal tine on the outer side, front view. Overstrand, B.M. (G.D.), M. 6384. $\frac{1}{4}$ natural size. C. *E.* sp. Basal portion of a right antler from East Runton. B.M. (G.D.), M. 6387. $\frac{1}{4}$ natural size. D. *E. ctenoides ?* Fragment of an antler from East Runton. B.M. (G.D.), M. 6395. $\frac{1}{4}$ natural size. E. *E. ctenoides ?* Fragment of an antler. East Runton. B.M. (G.D.), M. 6351, $\frac{1}{4}$ natural size. F. *E. sedgwicki*, antler of a young specimen, Bacton. B.M. (G.D.), Savin 2206. $\frac{1}{4}$ natural size. G. *E. ctenoides ?* Fragment of the upper portion of an antler. No locality. B.M. (G.D.), Savin 898. $\frac{1}{4}$ natural size.

97 ; pl. 7, fig. 3), who did not determine them. Two other specimens of the same species were attributed to *Cervus carnutorum* Laugel and to *Cervus ardeus* Croizet & Jobert by Newton (1891 : 25–26, pl. 4, figs. 3, 6).

The relationships between *E. falconeri* and *E. sedgwicki* are very close. They are both distinguished by the high position of the first bifurcation and by the well-marked flattening of the upper portion of the antlers. Very probably *E. sedgwicki* is the descendant of its older ally, from which it is distinguished only by more advanced characters, namely, the larger size, the greater number of the tines and their more pronounced flattening.

The relationships with *E. boulei* (Teilhard & Piveteau, 1930) are also very close. In *E. boulei* the flattening is confined to the upper tines; its range of variation seems to be very wide.

The relationships of *E. sedgwicki* with *E. dicranios* from the Upper Valdarno (Azzaroli, 1948) seem to be less close. The range of variation of this species is little known ; but it is always distinguished by the low position of the brow tine, by a peculiar backward bending of the upper tines and by their low grade of flattening. The tines of its lectotype are more numerous than in the type of *E. sedgwicki*.

The few specimens from Olivola (see also above, introduction to the genus *Euctenoceros*) do not agree perfectly with those of the Upper Valdarno. In the more complete skull (Azzaroli, 1948, fig. 10) the first bifurcation is set 8 cm. above the burr, and in the antler (fig. 8, incorrectly determined *E. ctenoides*) the backward bending of the upper tines is less pronounced. These specimens are probably slightly older than those from the Upper Valdarno (Azzaroli, 1950). *E. dicranios* may also be a descendant of *E. falconeri*; the question however is still open. The frontal from St. Prest, figured by Gervais (1867–69, pl. 16, fig. 4) and determined as *Cervus* (*Megaceros*) *carnutorum* Laugel, might possibly belong to *E. sedgwicki*. The name *Cervus carnutorum* was based on fragments of different species and should be dropped (Stehlin, 1912).

### **Euctenoceros,** *incertae sedis*

(Figs. 17 C, E, 21 B–E, G, 22)

Three lower jaws and a maxilla from East Runton and Sidestrand might be attributed indifferently to *E. ctenoides* or *E. sedgwicki*. *E. sedgwicki* is not otherwise recorded with certainty from these localities. The teeth are slightly larger, broader and more brachydont than those of *E. tetraceros*; the upper molars bear a discontinuous cingulum.

A large basal fragment of an antler from East Runton is rather puzzling (Fig. 21 C). It strikingly recalls *E. dicranios* from the Upper Valdarno.

Two bifurcated tines from the same locality (Fig. 21 D, E) might perhaps be attributed to *E. ctenoides* but are very imperfect

An upper portion of an antler (Fig. 21 G), and two similar fragments, from East Runton and Overstrand, may be attributed indifferently to *E. ctenoides* or to *E. sedgwicki* (cf. the two antlers of *E. ctenoides* in the Museum at Basel, figured by Kunst, 1937 : 42).

An antler from Overstrand (Fig. 21 B), with an abnormal outer tine near the base of the second tine, might also belong to *E. ctenoides*.

A fragment of a frontal with an abnormally reduced antler from East Runton (Fig. 22) affords an example of degeneration, probably due to very old age. The antler is much thinner than the pedicle and is reduced to a forked stump. Among the species from this locality, *E. tetraceros*, is, for its size, the only one to which this fragment might be attributed. Also a skull-roof from the same locality, with shed antlers (B.M. (G.D.), M. 6300), might belong to *E. tetraceros*. This specimen is of little interest. Its supraoccipital crest is weak.

A fragment of an antler attributed to "*Alces latifrons*" by Reynolds (1933, fig. 6*b*) might possibly belong to *E. sedgwicki*.

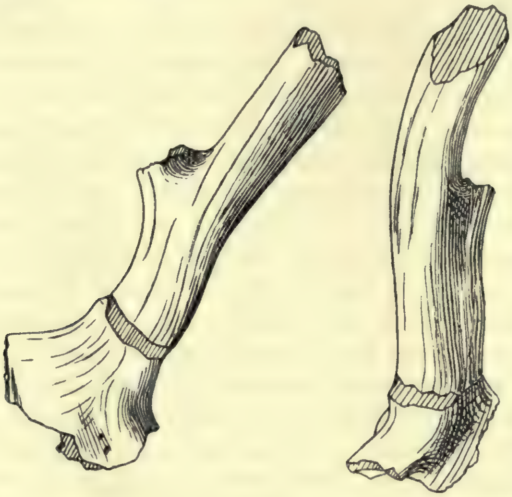

FIG. 22. *Euctenoceros ?* sp. Basal portion of a left antler. Abnormal specimen, presumably very old. East Runton, B.M. (G.D.), Savin 1776. ¼ natural size.

MEASUREMENTS:—

| Lower jaw: | Sidestrand.<br>B.M. (G.D.) Savin 1615 |
|---|---|
| Total length of the tooth row | 141 |
| Breadth of $M_2$ | 18 |

| Skull roof— | East Runton.<br>B.M. (G.D.) M. 6300 |
|---|---|
| Occipital breadth | 135 |
| Occipital height | 84 |
| Minimal frontal breadth *ca.* | 146 |
| Breadth of condyles | 81 |

## Genus ***MEGACEROS*** Owen

Many species more or less closely related to the familiar giant deer have been described in the last decades. They have generally been united under the name

*Megaceros*, alternately taken as a full genus or ranked as a subgenus of *Cervus*. Some terminal forms from North Africa and Eastern Asia have been separated under the subgenera *Megaceroides* Lydekker and *Sinomegaceros* Dietrich.

It is easily seen that this group is characterized by peculiar features of the skull, the antlers, the dentition and the limb bones; and although it is a plesiometacarpal, it widely differs from the other *Cervinae*. It is consistent therefore to give it full generic rank.

*Megaceros* is characterized by its large size, heavy build, large antlers, which generally are more or less palmated, and by a strange hyperostosis of the mandibular ramus and in a lesser degree of the skull, which eventually leads to monstrous forms. The significance of this hyperostosis has puzzled many palaeontologists, who often considered it a mark of degeneration or even a pathological character. However its occurrence in all the species of this genus gives evidence that it is not pathological in the common signification of the word; the more so as in the most widespread species it does not display any particularly wide range of variation. On the other hand it can hardly be considered a useful character, but always has a distinct mark of abnormality. Much light has been thrown on this point by Young's studies on *Megaceros pachyosteus* (1932), a very abundant species from the *Sinanthropus* site at Chouk'outien and other localities of Central China. In this species, which obviously belongs to a terminal branch, the hyperostosis is extreme. At the same time it displays a very wide range of variation, both in degree and in the way it affects the bones, and is accompanied by characteristic marks of degeneration, namely a shortening of the muzzle, small body size with an unusually wide range of variation, and the frequent occurrence of distinctly dwarf individuals. Young came to the conclusion that " . . . in the case of *Cervus pachyosteus* we witness a zoological group in some state of high zoological instability (or ' affolement '), this condition being due to a factor (the hyperostosis) which can be called a morbid one, since it was not directed to the formation of useful features."

Zdansky (1925–27) attributed the hyperostotic bones to various genera, but according to Young these identifications are incorrect.

Similarly degenerate characters (an extreme degree of hyperostosis, a very marked shortening of the muzzle and a small size) are displayed by another terminal form, *M. algericus* Lydekker (in Arambourg, 1938). This hyperostosis, as will be shown later, is well developed even in the earliest representatives of this genus in Europe, and there is no evidence of an increase of it with time.

An attempt to trace the phylogeny of the giant deer was made by Soergel (1927), who ranged the species in a unique phyletic line and assumed that they were derived from a Pliocene or Lower Pleistocene ancestor from N. Italy, *Cervus pliotarandoides* Alessandri. Soergel based his observations mainly on the antlers, and came to the conclusion that their evolution, starting from an hypothetical Pliocene ancestor with two basal tines (which he homologized with the brow and the bez tine of the red deer) was characterized by the disappearance of the lower (brow) tine and by a gradual downwards shift of the upper (bez) tine till close to the burr.

Many data have been made known since, and Soergel's conclusions need revision.

First of all, a strict homologizing with the brow and bez tine of the red deer is not possible. The antlers of *Megaceros* are built on a peculiar plan, very different from that of *Cervus* and the other *Cervinae*. We shall follow here the current nomenclature and refer to the fairly constant basal tine as the brow tine. Some species occasionally develop an inconstant additional tine below it, which will be referred to as the accessory basal tine. Moreover, the chronological sequence is not in accordance with Soergel's views.

The species of giant deer recorded in the literature are very numerous. Many of them, of course, are poorly known and of questionable value, but the better known species can easily be divided into two groups.

The skulls of the older species consist only of more or less complete brain cases. The antlers as a rule vary greatly; both skulls and antlers however give very valuable information on the relationships of the species. The teeth afford good examples of evolutionary progress with time, but seem to have advanced along parallel lines and are therefore of a more restricted use in classification. Moreover, their identification with skulls and antlers is sometimes uncertain.

The limb bones are robust. Young pointed out the broad form of the distal epiphysis of the metapodials in *Megaceros pachyosteus*. This character, although less pronounced than in the reindeer, is quite distinct and seems to occur in all the species of this genus. It has not yet been possible to establish whether limb bones may give some indication for classification.

The two groups into which this genus can be divided will be called, from their best known representatives, the group of *Megaceros giganteus* (= *M. euryceros* Aldrov.; for the priority of the name see Berckhemer, 1941) and the group of *M. verticornis* Dawk. The subgenera *Megaceroides* and *Sinomegaceros* mentioned above probably represent terminal branches of each group, but their relationships with the European species are not known with sufficient detail. Moreover the value of *Sinomegaceros* has been questioned by Teilhard (1936). These two subgeneric names therefore will not be used here.

### *The Group of* Megaceros giganteus

Pedicles divergent, but generally set near one another. Forehead hollowed in front of the pedicles (Fig. 23 D), and eventually swollen into a prominent transverse ridge between them. Brow tine branching off closely near the burr, flattened and more or less expanded, fluctuating in some of the younger species.

To this group I attribute: *Megaceros giganteus* Blumenbach; *M. antecedens* Berckhemer; *M. savini* Dawkins; *M.* sp. from Felixstow, Red Crag, East Anglia; *M. pachyosteus* Young; *M. ordosianus* Young; *M. flabellatus* Young; *M. yabei* Shikama.

*Megaceros giganteus* is the largest and most advanced species of this group, and is very familiar to palaeontologists. It was very widespread through Europe during the last interglacial and glacial phases. According to Mitchell & Parkes (1949), the Irish race was an inhabitant of grassy lowlands and the period of its maximal spread coincides with a mild Würm Interstadial, corresponding to the Alleröd stage of Denmark; it seems to have become extinct with the last cold phase. The races of Central and Southern Europe had presumably the same habits of life. I have not been able to find satisfactory information on their chronological range, but there is no evidence that any of them outlived the last glaciation (see also Frentzen & Speyer, 1928).

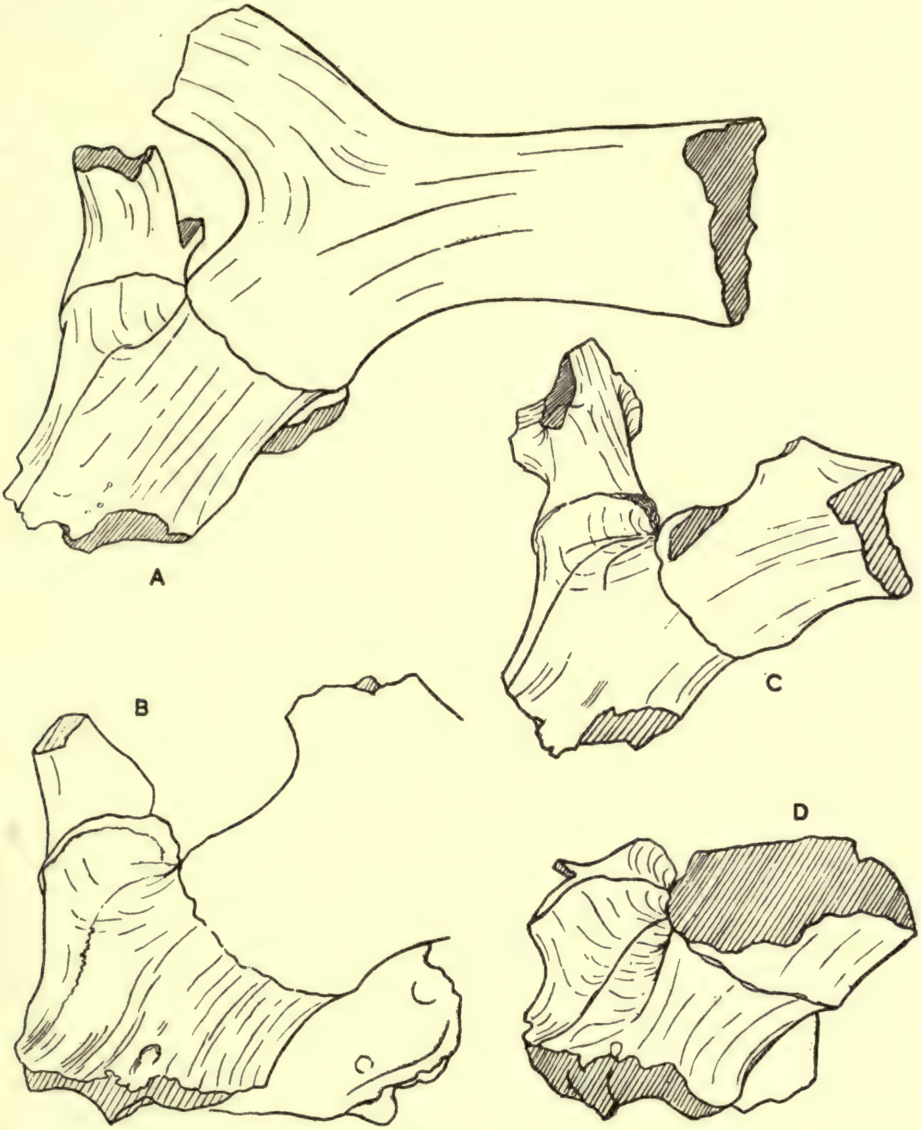

FIG. 23. Frontals of *Megaceros*, about $\frac{1}{3}$ natural size. A. *M. verticornis*, Pakefield. Norwich Museum 365. B. *M. verticornis*, Kessingland. Norwich Museum 364. C. *M. dawkinsi*, Sidestrand, B.M. (G.D.), M. 6302. (See also Fig. 33A.) D. *M. savini*, Kessingland. Norwich Museum 321.

Further references to this species may be found in Cornalia (1858–71), Pohlig (1892), Pavlow (1906), Hescheler (1909), Fabiani (1919), Frentzen & Speyer (1928), Reynolds (1929), Zakrewska (1932, 1935), Kunst (1937), Kirchner (1937), Azzaroli (1948). Pohlig distinguished three races, *hiberniae*, *germaniae* and *italiae*, based on antler characters. This distinction has not been accepted by all authors. Recently Kirchner rejected it, claiming that their ranges of variation widely overlap, but I am unable to accept his views. I grant that the variation is great and that extreme variants may eventually overlap, but on the whole Pohlig's specimens from Germany are quite distinct from the Irish specimens, and the distinctive characters listed by this author hold good, at least in a statistical sense. This is true also for the specimens described by Frentzen & Speyer. In discussing the range of variation of the German race Kirchner made reference to an incomplete antler from Bergrheinfeld a. Main, which actually seems to fit better with the Irish race; but its age is somewhat uncertain, possibly younger than Pohlig's specimens, and it cannot be taken therefore as a good representative of the German race.

The distinction of the Italian race is less clear, owing perhaps also to the incompleteness of the record. The identifications with Pohlig's races, made by some authors for specimens from other districts, are questionable. No doubt more detailed information on the age of the specimens will throw much light on their relationships and on the value of these smaller systematic units.

*Megaceros antecedens* from the *antiquus*-horizon of Steinheim a.d. Murr (a mild Riss interstadial; Berckhemer, 1941) has been described as a subspecies of *M. giganteus*, but I prefer to give it full specific rank. It is smaller than *M. giganteus* and its dentition is more primitive. The antlers are stout, little divergent and broadly palmated. The brow tine is expanded into a small palmation. A related form, not yet well defined, occurs in the overlying *primigenius*-horizon.

*Megaceros savini* from the Forest Bed is still more primitive. The brow tine is widely expanded, the beam is long and flattened and ends with three tines. This is the only example of the lack of a palmation in the genus *Megaceros*. The dentition is primitive. A more detailed description will be given later.

*Megaceros* sp. ind. from the Red Crag at Felixstow is represented by a basal fragment of an antler, described and figured by Owen (1856, fig. 18), and is now in the Museum at Ipswich. It is a very poor fragment. The brow tine is broken; its base lies close to the burr and is slightly expanded, as in *M. giganteus*; the beam shows the same sigmoidal swing. For these reasons I attribute it to this group. There is no certain information about the horizon of this specimen. Its fossilization shows that it was derived possibly from the lower part of the Red Crag.

*Megaceros pachyosteus* (Young, 1932) was found at the *Sinanthropus* site at Chouk'outien and at other localities of Central China. At Chouk'outien it is extremely abundant. Its skull and antlers clearly show the characters of this group; it is distinguished by a relatively small size, a very brachyodont dentition, an extreme hyperostosis of the skull, and by other characters clearly pointing to degeneration. The skull is very broad and depressed, the muzzle short, the body size is very variable and distinctly dwarf individuals are not uncommon. Also the antlers are very variable, but are always very stout and broadly palmated. The brow tine is also palmated. The dentition is still rather primitive.

*Megaceros ordosianus* from the loess of Manchuria, *M. flabellatus* from locality 9 at Chouk'outien and *M. yabei* from the Upper Pleistocene of Japan (Young, 1932; Teilhard, 1936; Shikama, 1939) are distinguished from *M. pachyosteus* by a less developed hyperostosis and by some characters of the antlers. According to Teilhard the wide range of variation makes specific distinctions somewhat difficult.

### *The Group of* Megaceros verticornis

Pedicles divergent, generally set wide apart and directed obliquely backwards. Forehead transversely flat or convex in front of the pedicles (Fig. 23), generally marked by two faint ridges running along the median bases of the pedicles and vanishing on the forehead. No transverse ridge on the skull roof between the pedicles. Brow tine typically subcylindrical, arising from the upper portion of the beam at some distance from the burr and strongly bent forwards. Very often a more or less distinct knob below it on the anterior part of the beam, which may eventually develop into an accessory tine, close to the burr. Some species display various degrees of reduction of the brow tine.

To this group I attribute *Megaceros verticornis* Dawkins; *M.* aff. *verticornis* from Süssenborn; *M.* aff. *verticornis* from Trimley, Red Crag; *M. dawkinsi* Newton; *M. belgrandi* Lartet from Montreuil (= *M. dawkinsi*?); *M.* aff. *belgrandi* from Taubach; *M.* aff. *belgrandi* from Laufen; *M.* aff. *belgrandi* from Tiraspol; *M. mosbachensis* Soergel; *M. solilhacus* Robert; *M. algericus* Lydekker; *M. pliotarandoides* Alessandri; *M. cazioti* Depéret; *M. cretensis* Simonelli.

The fragment from the loess of Kalouga attributed to "*Cervus*" *verticornis* by Pavlow (1906: 39) is not a *Megaceros.*

*Megaceros verticornis*, to be described in detail below, is the best known species. It is nearly as large as the Irish giant deer, but more primitive in the dentition. The basal portion of the antlers shows a remarkable constancy both in the form and in the position of the brow tine. An accessory basal tine is quite exceptional. The upper portion of the antler is broadly palmated, with a faintly scalloped edge.

*Megaceros* aff. *verticornis* from Süssenborn (Soergel, 1927) differs from the above species by the presence of tines on the anterior edge of the palmation (the posterior portion is destroyed). This might be perhaps a merely individual character. The dentitions of these species are nearly identical.

*Megaceros* aff. *verticornis* from the Red Crag at Trimley (Dawkins, 1887) is represented by an imperfect shed antler. This antler is very stout but does not differ otherwise from those of *M. verticornis* from the Forest Bed. Dawkins identified it with this species, and were it not for its older age I also should not hesitate to do so. The fossilization shows that this specimen is contemporary with the Crag, but there is no exact information on the horizon in which it was found.

*Megaceros dawkinsi* from the Forest Bed will also be described below. It is smaller than *M. verticornis*; its forehead is prominent and the pedicles are strongly directed backwards. The antlers are palmated, stout, small, and very variable in shape. The brow tine is fluctuating. I interpret these characters as due to a secondary reduction. The dentition is hypsodont but with primitive features.

*Megaceros belgrandi* from Montreuil near Paris, described and figured by Belgrand (1869); *M.* aff. *belgrandi* from Taubach (Pohlig, 1892); *M.* aff. *belgrandi* from the high terrace of the Neckar near Laufen, Schwaben (Dietrich, 1909); and *M.* aff. *belgrandi* from Tiraspol (partly determined as *M. belgrandi*, partly as *M. euryceros* by Pavlow, 1906, pl. i, figs. 4, 5) are all very imperfect. They might perhaps be identical with *M. dawkinsi*. According to Dietrich the specimen from Laufen is of Upper Pleistocene age; the others come from the Middle Pleistocene.

*Megaceros mosbachensis* from Mosbach (Soergel, 1927) agrees with *M. verticornis* in the characters of the skull but shows some divergence in the basal portion of the antlers. The peculiar upper brow tine is present only on the right side with an accessory tine below it; on the left side there is only this accessory tine. The teeth are massive and very broad. This species was based on a single specimen.

*Megaceros solilhacus* from the Middle Pleistocene of Solilhac, Haute Loire (Robert, 1829) is a very large species but with relatively small antlers. The palmation is narrow, the brow tine is more or less reduced. A very fine antler has been figured by Moullade (1886) and by Freudenberg (1914) under the name *Cervus dama priscus*. The dentition is advanced, and the hyperostosis of the lower jaw is poorly developed. This species inhabited the highlands of Central France during the Riss Glaciation. I shall give soon a new description of it.

*Megaceros algericus* from the Middle and Upper Palaeolithic of Algeria and the Mousterian of Morocco (Arambourg, 1938) clearly shows the skull characters of this group. It reproduces also some features of *M. pachyosteus*, namely the extreme degree of hyperostosis, the small size and the shortening of the muzzle. This is well seen in a fine skull in the Palaeontological Museum in Paris, not yet described.

*Megaceros pliotarandoides* from the Upper Pliocene or Lower Pleistocene of Cortiglione Monferrato, N. Italy (De Alessandri, 1903) is based on an incomplete shed antler. It shows in its basal portion the characters of the group of *M. verticornis* but is very unsatisfactory and its affinities are uncertain.

*Megaceros cazioti* from Corsica and *M. cretensis* Simonelli are dwarf island forms. A more detailed discussion of these species will be given in another paper.

There are in addition some remains whose affinities cannot be established:

*Megaceros dupuisi* from the Lower (or Middle ?) Pleistocene of Rosières, France (De Grossouvre & Stehlin, 1912), is represented by some lower jaws and very imperfect fragments of antlers. The teeth are identical with those I tentatively identify with *M. savini*.

*Megaceros* sp. A large metatarsal from Leffe, N. Italy (Stehlin, 1930) seems the only unquestionable evidence of the occurrence of this genus in the Villafranchian of Italy.

*Megaceros* sp. A lower jaw from the Red Crag, in the Museum at Ipswich, not yet described. The teeth are broken off and only a part of $M_1$ is preserved. The length of the tooth row is as in *M. verticornis* and the horizontal ramus is very thick: its height below $M_2$ is 50 mm., its breadth 40 mm. The fossilization shows that this specimen was derived presumably from the lower part of the Red Crag.

*Megaceros* sp. from St. Prest is possibly identical with *M. dupuisi* (Stehlin, 1912: 206).

*Megaceros* cf. *dupuisi* from Csarnòta and Püspökfürdö (Schaub, 1932) is also very poorly represented.

A few giant deer have been described also from Switzerland (see Hescheler & Kuhn, 1948: 190–192). One of them, from the Wengimoos near Berne, is remarkable for the shortness of its neck, and is supposed to be post-glacial.

Several imperfect remains of giant deer have also been made known from Middle Pleistocene deposits of England. They all belong to more primitive species than *M. giganteus.*

According to Stehlin (1932 : 143) *Cervus martialis* Gervais (1859 : 144, pl. 21, fig. 1–8) is also a *Megaceros.* I do not feel certain of this. The lower jaw (Gervais' fig. 1) is certainly of a giant deer, but the antlers seem rather to belong to a relative of *Euctenoceros sedgwicki.*

*Megaceros messinae* Pohlig (1909) from Sicily seems to be another dwarf island form.

### ***Megaceros verticornis*** (Dawkins)

(Figs. 23 A, B, 24–27, 28 M, N, 29 E, F, 30, 32 B, C.)

1872. *Cervus verticornis* Dawkins (pars), p. 405, fig. 2.
1882. *Cervus verticornis* Dawkins : Newton, p. 61.
1887. *Cervus verticornis* Dawkins : Dawkins (pars), pl. 5, figs. 1–3 ; pl. 6, figs. 1, 2 ; pl. 7, figs. 1, 2.
1891. *Cervus verticornis* Dawkins : Gunn (pars), pl. 2, fig. 97.
1891. *Cervus verticornis* Dawkins : Newton, p. 32.
1899. *Cervus belgrandi* Lartet : Harmer, p. 97, pl. 21.

SYNONYMY. The definition of this species has been discussed by Newton. Dawkins, in his original description, included in it also an antler on which Newton later based his *Cervus dawkinsi.* Newton chose as the type of *C. verticornis* the basal fragment of an antler from Pakefield, figured by Dawkins (1872, fig. 2).

In his later description (1887) Dawkins again included in *C. verticornis* some remains of other species. On p. 23 he recorded seven specimens with a double basal tine; exact reference was made only to a specimen in the British Museum, registered B.M. (G.D.), 33471. This register number includes a small sample of very imperfect fragments, none of which belongs to *Megaceros verticornis.* A double basal tine is quite exceptional in this species: I do not know the other specimens quoted by Dawkins, but as yet I have seen only a fragment of a young individual from Trimingham with a well-developed accessory basal tine (Fig. 26). This specimen was found after the publication of Dawkins' works.

The antler from the Red Crag at Trimley figured by Dawkins (1887, pl. 6, fig. 3) is imperfect and cannot, since it is older, be identified confidently with *M. verticornis.* The fragment from Kessingland figured by Gunn (pl. 7, fig. 2) is doubtful; it does not seem to belong to *M. verticornis.*

OCCURRENCE. This is the commonest species of *Cervidae* in the Forest Bed and has been recorded from nearly all the fossiliferous localities: Kessingland, Pakefield, Mundesley, Overstrand, Happisburgh, Trimingham, Hopton, Sidestrand, Bacton, Cromer; it is common also in the Upper Freshwater Bed at West Runton, but is not recorded at East Runton.

The remains of this species consist for the most part of basal fragments of the antlers, either naturally shed or with fragments of the frontals. There are in addition two complete brain cases, one in the Norwich Museum (Figs. 24, 25), the second in the British Museum (Fig. 27). The latter was found in connection with the atlas, the axis and the antlers, nearly perfect, and has been described by Harmer under the name *Cervus belgrandi*, of which *Cervus verticornis* was incorrectly supposed to be a synonym.

A shed antler, in the Museum of the Geological Survey, figured by Dawkins (1887, pl. 5, fig. 2), is broken at the beginning of the palmation.

The correlation between skulls and teeth is based on the size, on their occurrence together in the Upper Freshwater Bed at West Runton, where no other species of *Megaceros* has as yet been found, and on comparison with *M.* aff. *verticornis* from Süssenborn. The dentition is represented by some lower jaws and maxillae.

Some limb bones may also possibly belong to this species.

Description. *Skull:* There is very little to add to Harmer's description of the skull from Pakefield. Harmer pointed out its large size and heavy form, its flat forehead and its divergent and widely spaced pedicles. The supraorbital foramina are very large and round. Two very faint ridges, starting from the coronal suture, run along the inner margins of the pedicles and vanish on the forehead. In other specimens these ridges are better developed (Fig. 25). Harmer also pointed out the lack of a transverse swelling of the frontal between the pedicles.

The other remains of skulls display little individual variations. The pedicles are generally widely spaced, but in a frontal from Pakefield (Figs. 23 A, 25 D) they are set near each other and less divergent than in the average specimens. The frontal is still flat.

*Antlers:* The characters of the lower portion of the antlers are remarkably constant. The brow tine arises at some distance above the burr, from the upper portion of the beam, and is strongly bent dowwards. It is rounded in cross-section and very long in a skull from Kessingland (Dawkins, 1887, pl. 7, fig. 2), the only specimen where it is complete. In many specimens there is a more or less marked knob below it, on the anterior side of the beam; this may be present on both sides or on one side only and is very variable. In a frontal from Trimingham, very much worn, it is very strong on the left side and seems to be completely lacking on the right side, but only in a young antler (Fig. 26), also from Trimingham, has it developed into an accessory lower tine. Dawkins' statement that an accessory lower tine occurs in seven other specimens has not been fully checked, but is based partly at least on incorrect identifications.

The beam is long and bears an anterior and a posterior tine, ovoidal in cross-section. The position of the anterior tine is somewhat variable (see Figs. 25 C, 27, and the figures published by Dawkins, 1887). An additional anterior tine has been recorded only in one instance (Dawkins, 1887, pl. 5, fig. 3). Above the posterior tine the beam is twisted upwards and becomes flattened, and after a short distance

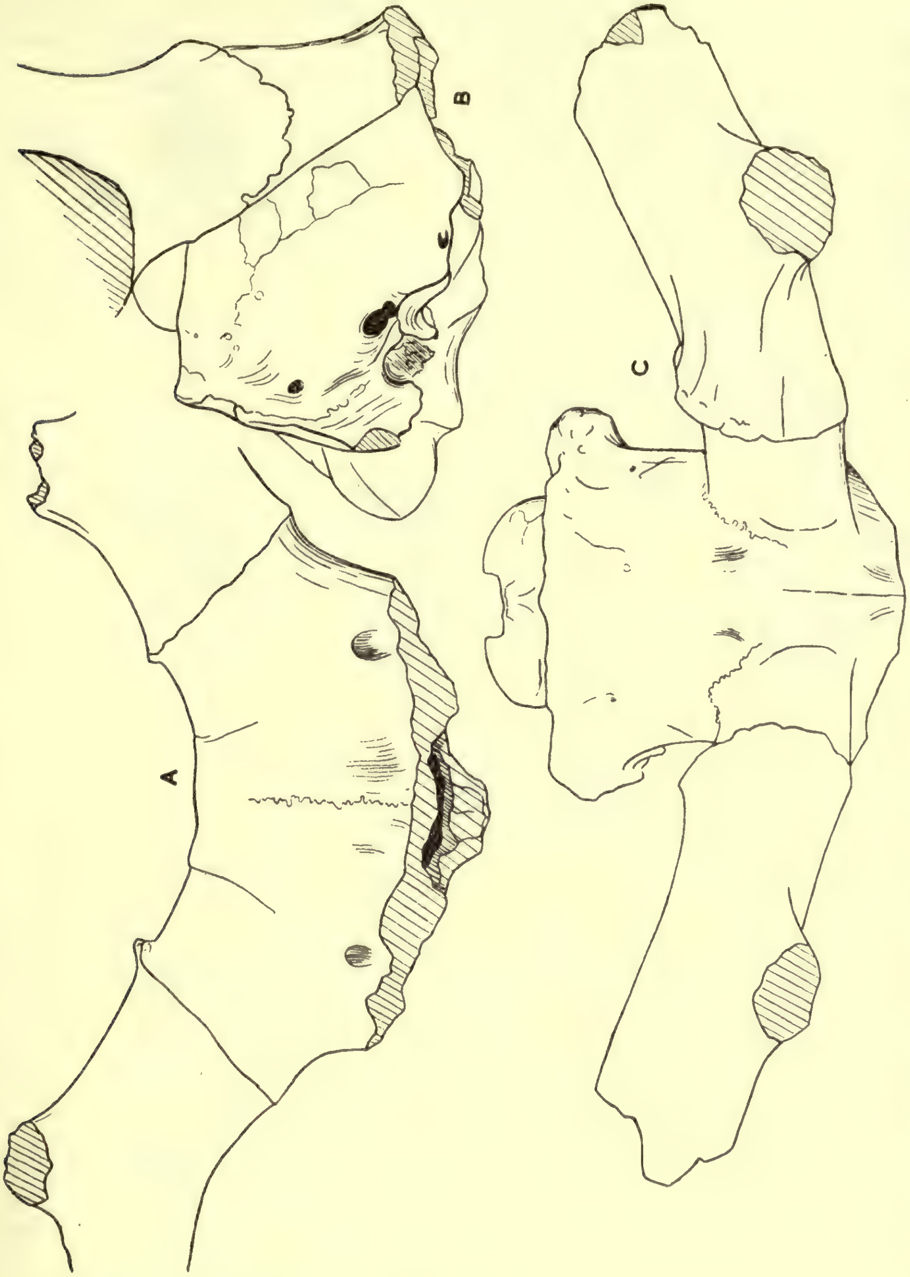

Fig. 24. *Megaceros verticornis*, skull from Kessingland. Norwich Museum 364. ⅓ natural size. (See also Figs. 23 & 25.) A. Anterior aspect. B. Lateral aspect. C. Dorsal aspect.

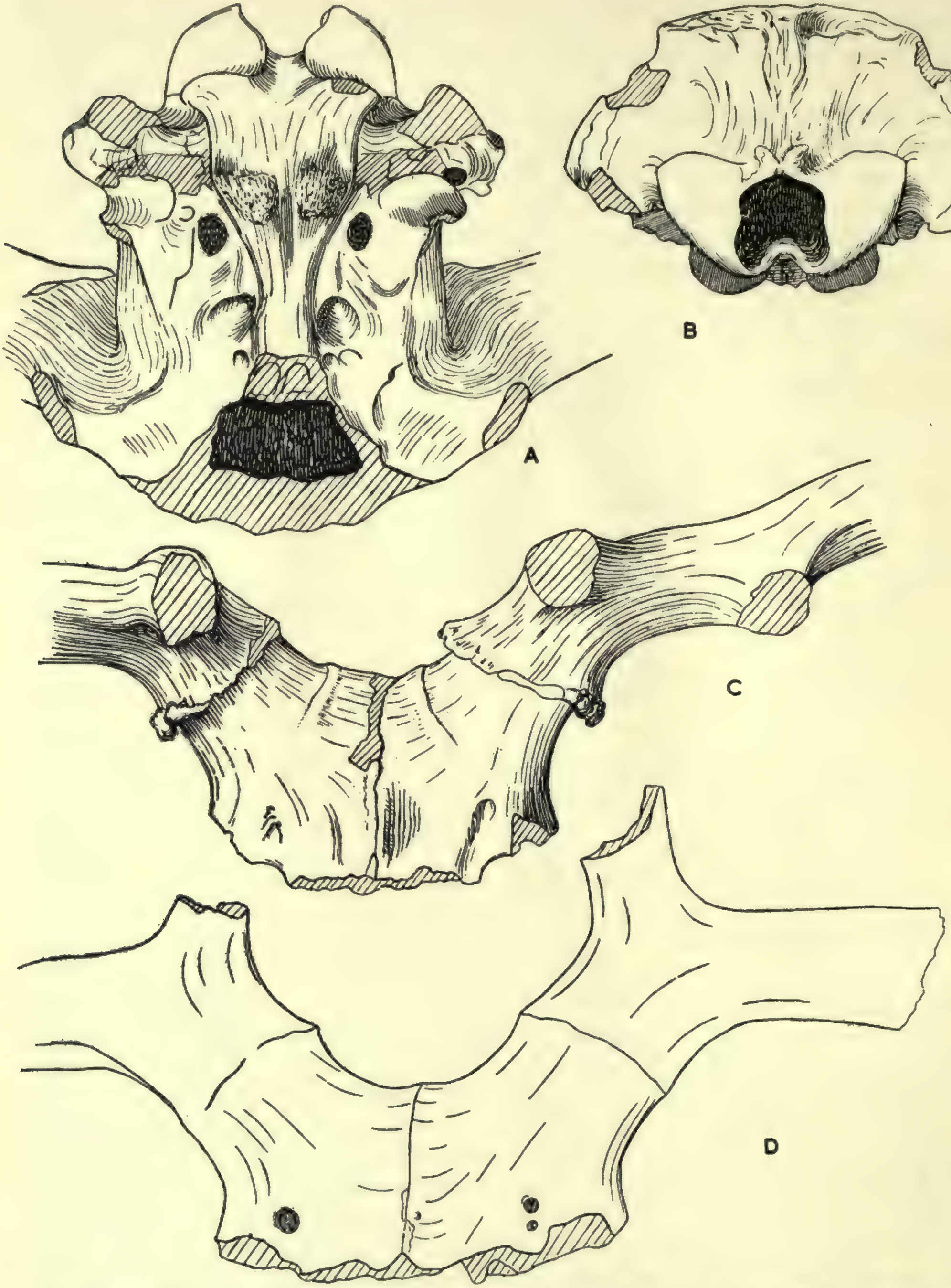

FIG. 25. *Megaceros verticornis*, skulls. A. Inferior aspect, from Kessingland. Norwich Museum 364. (See also figs. 23 & 24.) B. Posterior aspect, same specimen. $\frac{1}{3}$ natural size. C. Anterior aspect. West Runton, Upper Freshwater Bed. B.M. (G.D.), M. 6099. $\frac{2}{9}$ natural size. D. Anterior aspect. Pakefield, Norwich Museum 365. $\frac{1}{3}$ natural size.

it suddenly expands into a palmation. This palmation is preserved only in Harmer's specimen, so that we have no information on its variations. It is very broad and thin and of a quite unusual pattern: its margin does not give origin to long tines as in most of the giant deer, but is scalloped and gently bent inwards. The anterior edge was destroyed on both sides. The plane of the palmation is nearly vertical and set at 45° with the median plane of the body. The total span in the reconstructed specimen is 228 cm. Harmer also pointed out the rectilinear course of the blood vessels.

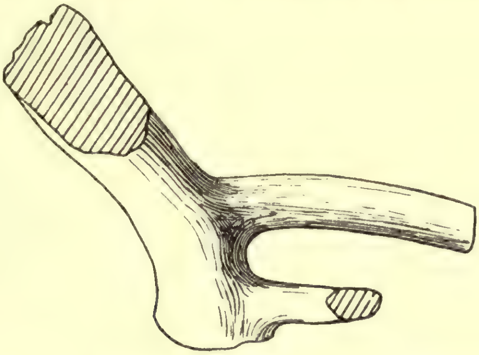

FIG. 26. *Megaceros verticornis*, young specimen with an abnormal lower tine, Trimingham. B.M. (G.D.), Savin 713. ⅓ natural size.

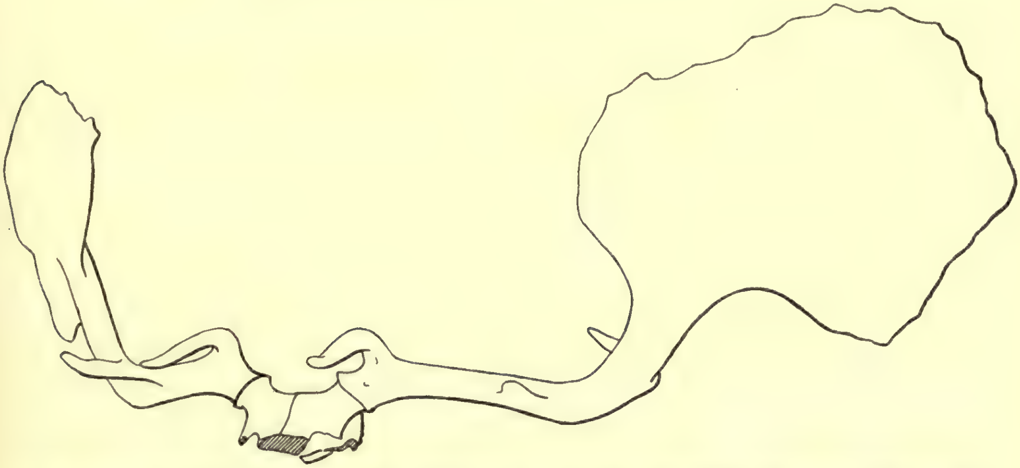

FIG. 27. *Megaceros verticornis*, reconstruction of the specimen described by Harmer (1899), Pakefield. B.M. (G.D.), M. 11352. $\frac{1}{14}$ natural size.

Harmer's specimen is rather large, but the lectotype and the skull from the Upper Freshwater Bed of West Runton (Fig. 25 c) slightly exceed it. The antler figured by Dawkins, 1887, pl. 5, fig. 2, the most complete beyond Harmer's specimen, is on the contrary distinctly smaller.

*Dentition:* The remains consist of a maxilla and two lower jaws from the Upper Freshwater Bed at West Runton, a maxilla from Trimingham and some imperfect lower jaws from Pakefield, in the British Museum; a maxilla from Kessingland and probably two lower jaws, from Copton and Kessingland, in the Norwich Museum.

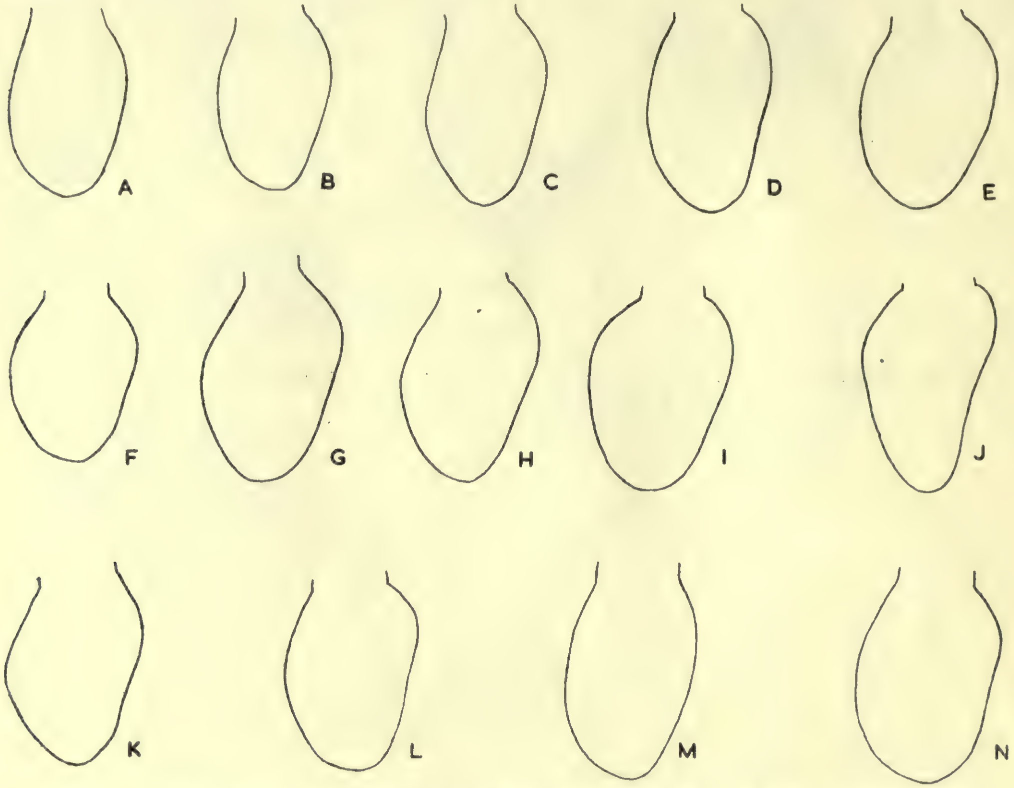

Fig. 28. Cross-sections of lower jaws, below hinder lobe of M2. External side to the left. $\frac{2}{3}$ natural size. A–I. *Megaceros dawkinsi.* A. Mundesley, B.M. (G.D.), M. 6335 (young). B. Overstrand, B.M. (G.D.), Savin 533. C. Sidestrand, B.M. (G.D.), M. 6224. D. Overstrand, B.M. (G.D.), M. 6209. E. East Runton, B.M. (G.D.), Savin 304. F. Mundesley, B.M. (G.D.), M. 6207 (old). G. Overstrand, B.M. (G.D.), Savin 526. H. Mundesley, B.M. (G.D.), Savin 339. I. Pakefield, B.M. (G.D.), M. 6501. J. Cervid indet., Overstrand. B.M. (G.D.), Savin 421. K & L. *Megaceros savini ?* K. Trimingham, B.M. (G.D.), M. 6220. L. Mundesley, B.M. (G.D.), Savin 1008 (old). M & N. *Megaceros verticornis.* M. Overstrand, B.M. (G.D.), Savin 1198. N. West Runton, Upper Freshwater Bed. B.M. (G.D.), Savin 1069.

The hyperostosis of the lower jaw is moderate (Fig. 28). The teeth are relatively small and narrow. The basal columns are moderately developed, and in the maxilla from West Runton the upper premolars show a very faint trace of a cingulum. $P_4$ is somewhat intermediate between the primitive and the advanced condition. The enamel is moderately thick, the height of the crown also moderate.

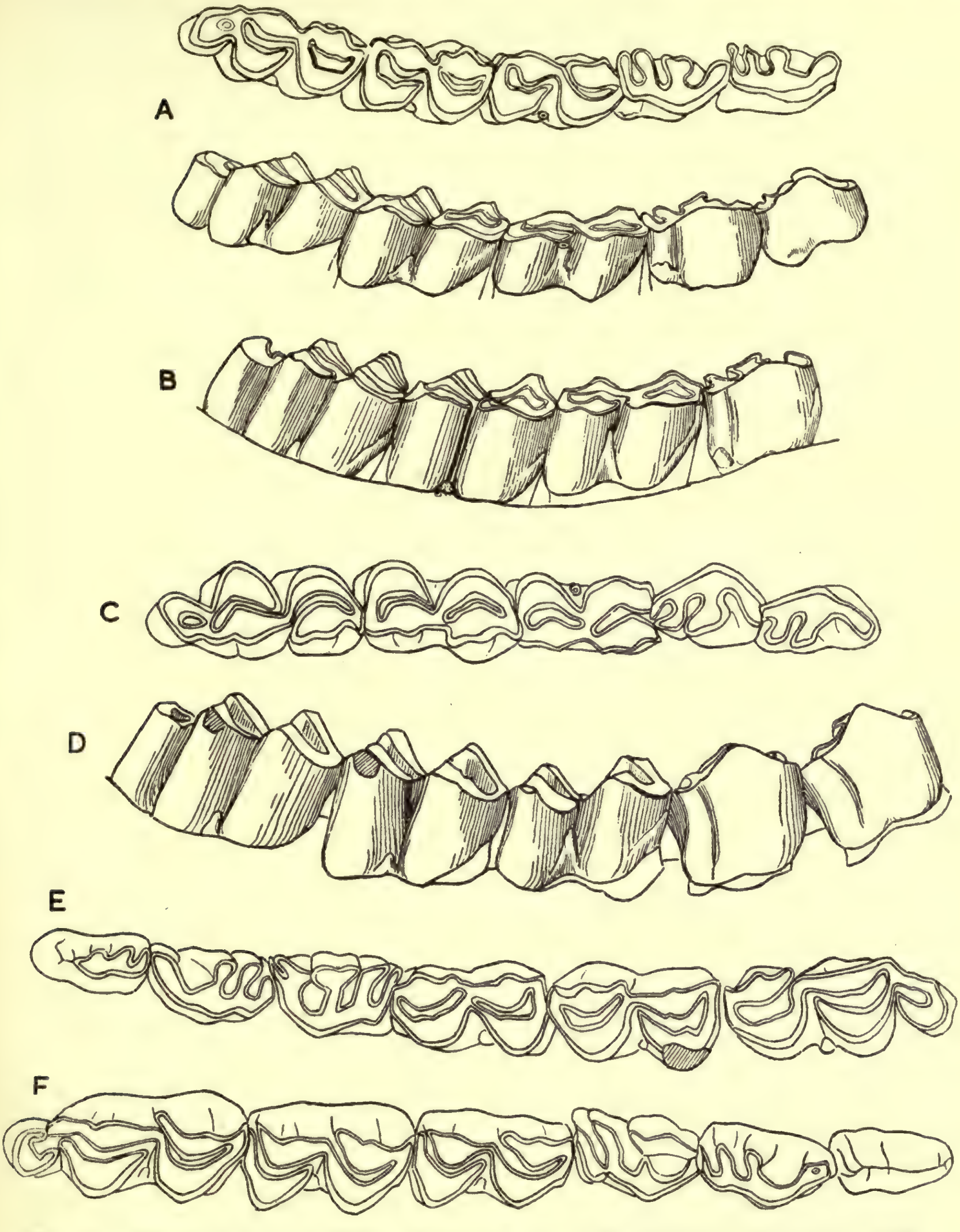

Fig. 29. *Megaceros*, lower dentition, $\frac{10}{11}$ natural size. A. *M. dawkinsi*, Overstrand. B.M. (G.D.), Savin 533. B. *M. dawkinsi*, Mundesley. B.M. (G.D.), M. 6231 (young). C. *M. savini ?* Trimingham, B.M. (G.D.), M. 6207. D. *M. savini ?* Trimingham, B.M. (G.D.), Savin 439. E. *M. verticornis*, West Runton, Upper Freshwater Bed. B.M. (G.D.), Savin 1069. F. *M. verticornis*, West Runton, Upper Freshwater Bed. B.M. (G.D.), Savin 1265.

VERTEBRAE. Atlas and axis were found in connection with Harmer's specimen. They have already been described by Harmer and are slightly smaller than the corresponding bones of *Megaceros giganteus*, but very similar in shape.

COMPARISONS. The giant deer from Süssenborn, figured by Soergel (1927, pl. 17, fig. 2; pl. 18, figs. 2, 4, 7), is closely related to *M. verticornis*. The skull, the dentition and the lower portion of the antlers are identical. The upper portion of the antlers in the specimen from Süssenborn is flattened and gives off two large tines from the anterior edge; the posterior portion is destroyed. In Harmer's specimen from the Forest Bed the anterior edge of the palmation is missing on both sides, but what remains of it on the right side is very thin (15–20 mm.) and is not likely to have developed large tines, which moreover would be in contrast with the general pattern of the palmation.

The systematic value of these differences is not known, as we have no idea of the range of individual variation of these forms, but no doubt they are very closely allied.

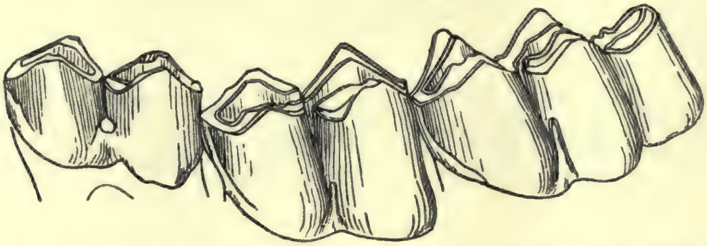

FIG. 30. *Megaceros verticornis*, lower molars, Pakefield. B.M. (G.D.), M. 6223. Natural size.

*Megaceros mosbachensis*, of which only a brain case with the lower portions of the antlers and some fragments of the dentition are known, also closely resembles *M. verticornis* in the characters of the skull, but differs in the antlers and teeth (see above).

The affinities between *M. verticornis* and *M. dawkinsi* are also very close and will be discussed later.

The lower jaw of *M. dupuisi* differs from that of *M. verticornis* by its smaller size and the more primitive form of $P_4$.

The affinities between *M. verticornis* and *M. giganteus* have been discussed by Harmer and by Soergel. It has already been shown that although these two species are related they belong to different lineages.

MEASUREMENTS OF THE TEETH :—

| | B.M. (G.D.), Savin 1156<br>W. Runton,<br>U. Freshw. Bed |
|---|---|
| Upper tooth row : | |
| Total length . . . . | 124 |
| Breadth of $M^2$ . . . . | 22 |

|  | B.M. (G.D.), Savin 1069 | B.M. (G.D.), Savin 1265 |
|---|---|---|
| Lower tooth row : | W. Runton, U. Freshw. Bed |  |
| Total length | 146 | 152 |
| Breadth of $M_2$ | 17 | 18 |

## ***Megaceros dawkinsi*** (Newton)

(Figs. 23 C, 28 A–I, 29 A, B, 31 A, 32A, 33–36.)

1872. *Cervus verticornis* Dawkins (pars), p. 405, fig. 1.
1882. *Cervus dawkinsi* Newton, p. 54.
1882. *Cervus fitchii* Gunn MS. : Newton, p. 56.
1882. *Cervus gunni* Dawkins MS. : Newton, p. 57.
1887. *Cervus dawkinsi* Newton : Dawkins, p. 7, pl. 2, figs. 1, 2, pl. 3, fig. 3.
1891. *Alces* ? : Gunn, pl. 5, fig. 6.
1891. *Cervus fitchii* Gunn, pl. 6, fig. 1.
1891. *Cervus dawkinsi* Newton : Newton, p. 26.
1891. *Cervus fitchii* Gunn : Newton, p. 28.

SYNONYMY. This species was founded by Newton on a young antler, formerly attributed to *Cervus verticornis* by Dawkins. Other fragments determined as *Cervus fitchii* and *Cervus gunni* by Newton belong to the same species, as already pointed out by Dawkins. Newton (1891) rejected this view, but in my opinion he overestimated differences due to individual variation.

OCCURRENCE. This species is nearly as abundant and widespread as *Megaceros verticornis* and has been recorded from Bacton, Cromer, Trimingham, Sidestrand, Mundesley, Overstrand, Pakefield, Walcot and East Runton (one specimen, much rolled). A specimen in the Savin collection was found at Weybourn and was supposed to come from the Weybourn Crag; its occurrence has been discussed in the previous section. *M. dawkinsi* has not been recorded from the Upper Freshwater Bed.

The specimens consist of several portions of antlers and fragments of the frontals ; a specimen from the Walcot gap, in the museum at Norwich, bears also a part of the left parietal and temporal bones, but no complete brain cases have been found. The correlation between antlers and teeth is based on the size. The dentition is represented by several lower jaws and few fragments of the maxillae.

DESCRIPTION. The skull is distinctly smaller than that of *Megaceros verticornis*, but is represented by rather unsatisfactory specimens, so that exact measurements are possible only for the frontals. Its most striking feature is given by the convex form of the forehead and by the backward inclination of the pedicles. In the adult the pedicles are short, very massive and strongly divergent. Two shallow ridges on their inner borders, as in *M. verticornis*, are always distinct. The skull roof of the specimen reproduced on Fig. 33 A is pierced by numerous small openings; its inner surface in this region has been filled with plaster. Similar openings have been described also by Soergel (1927) in the giant deer from Mosbach and Süssenborn; they were interpreted as canals for blood-vessels.

The antlers, of which the upper portion is unknown, are stout, palmated, and very variable. The beam is short and rounded. Its base, unlike that of *M. verticornis*, does not grow in the same direction as the pedicle but is stretched outwards and backwards, and is thinner than the pedicle. This is well seen also in a young specimen reproduced on Fig. 33 C. The brow tine and the accessory lower tine are very variable, but are always more or less reduced. The type affords the only instance of a well-developed lower accessory tine. Very often both these tines have disappeared. The upper tines are moderately flattened and gently twisted upwards.

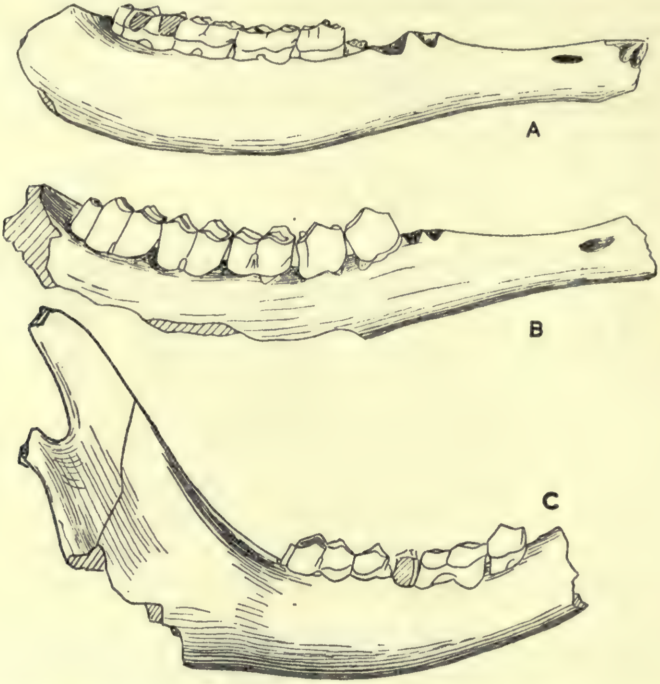

FIG. 31. *Megaceros*, lower jaws. ⅓ natural size. A. *M. dawkinsi*, Overstrand. B.M. (G.D.), Savin 526. B. *M. savini ?* Trimingham, B.M. (G.D.), Savin 439. C. *M. savini ?* Mundesley, B.M. (G.D.), Savin 1008.

There may be one or two anterior tines, and a posterior tine is not always present. The upper portion is more or less abruptly twisted upwards, sometimes resembling features of *M. verticornis*, sometimes as in Fig. 36, rather recalling *M. giganteus*. In the specimen shown on Fig. 23 C and 33 A the branching of the right antler takes place in two different planes: this is probably due to an unusual shortening of the beam between the anterior tine and the beginning of the palmation.

The teeth I refer to this species consist of several lower jaws, a fragment of a maxilla and some isolated molars. The dental characters recall those of *M. verticornis*; the teeth are however smaller, narrower, very hypsodont, and have a thick enamel. The lower molars bear strong basal columns and anterior folds. $P_4$ is always very primitive and is characterized by the poor development of its hinder portion ; the latter is bordered by a small burr near the base of its outer wall.

The hyperostosis of the lower jaw is well marked (Fig. 28).

AFFINITIES. Dawkins (1887) pointed out the general resemblance of the antlers with those of *M. giganteus*, but concluded that the affinities between these two species are not very close.

As he limited his observations to the antlers, he failed to perceive the affinities between *M. dawkinsi* and *M. verticornis*, which moreover was imperfectly known until the discovery of Harmer's specimen, ten years later.

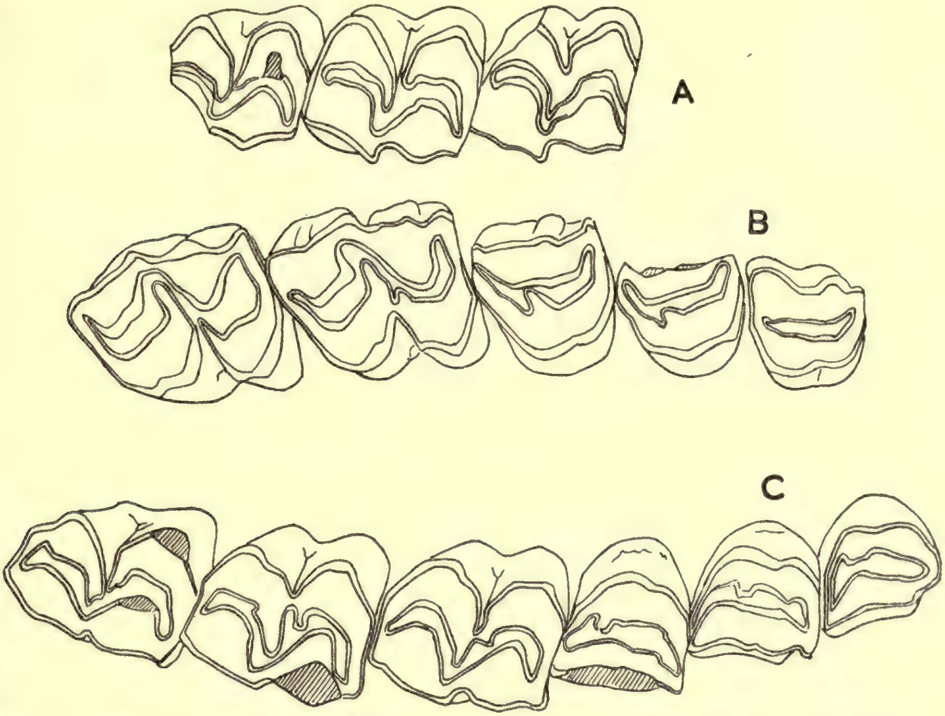

FIG. 32. *Megaceros*, upper dentition. Natural size. A. *M. dawkinsi*, Trimingham, B.M. (G.D.), Savin 7. B. *M. verticornis?* Trimingham, B.M. (G.D.), Savin 942. C. *M. verticornis*, West Runton, Upper Freshwater Bed. B.M. (G.D.), Savin 1156.

The characters of the skull leave little doubt that *Megaceros dawkinsi* belongs to the group of *M. verticornis*. The antlers support this conclusion: it has been shown that a small brow tine, similar to that of *M. verticornis*, is not uncommon. This never occurs in the group of *M. giganteus*.

However, *Megaceros dawkinsi*, in spite of its small size, is not primitive, and does not belong to the same lineage as *M. verticornis*. The dentition displays simultaneously primitive and advanced features; the lower pre-molars are perhaps of the most primitive pattern yet known, but both the hypsodonty and the thickness of the enamel are no doubt advanced features. There is no hint of the broadening

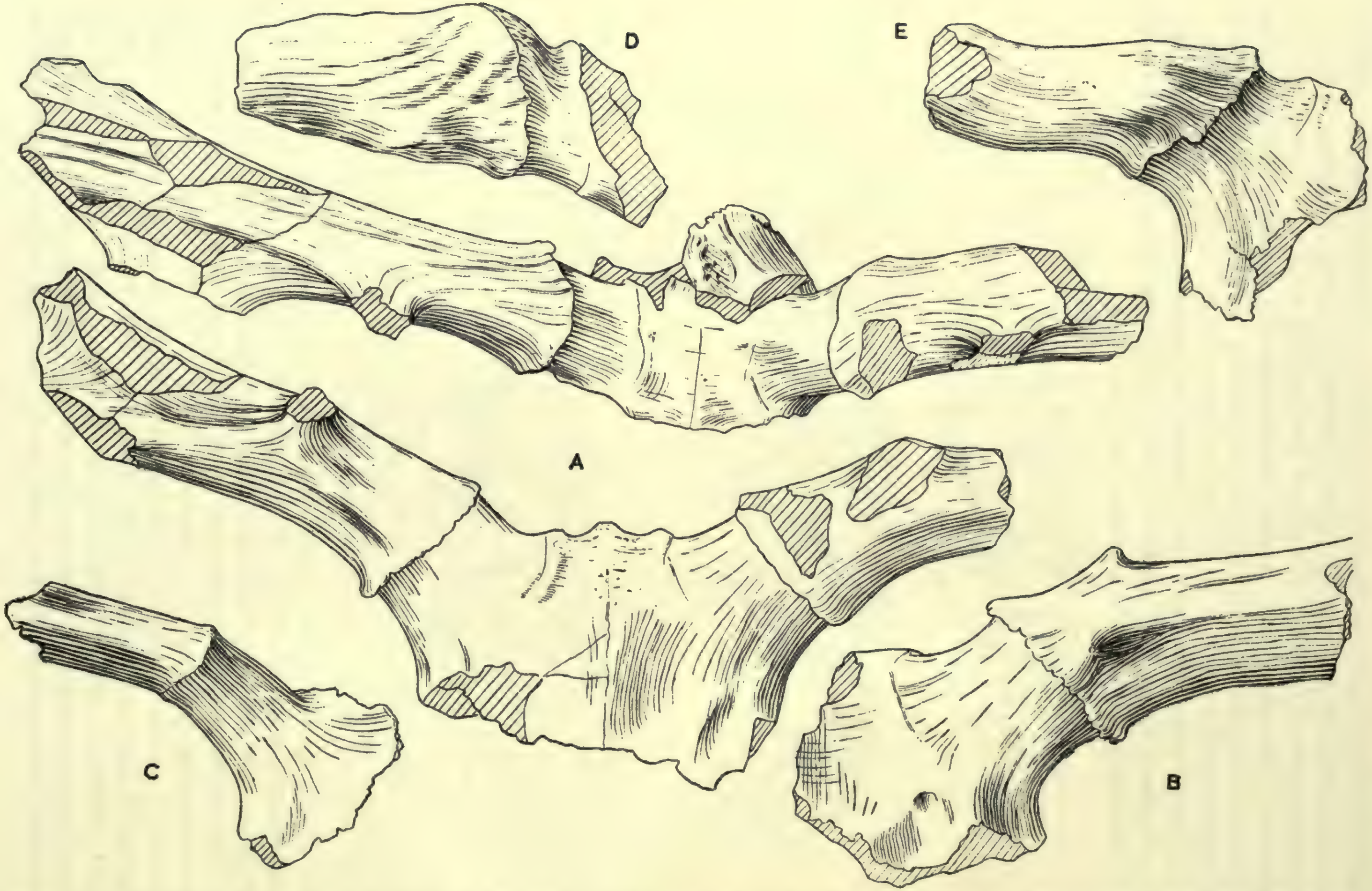

FIG. 33. *Megaceros dawkinsi*, parts of the skull. ⅓ natural size. A. Dorsal and anterior views. Sidestrand, B.M. (G.D.), M. 6302. (See also Fig. 23.) B. Anterior view. Mundesley, B.M. (G.D.), M. 6424. C. Anterior view. Mundesley, B.M. (G.D.), Savin 1883 (very young). D. Dorsal view. Trimingham, B.M. (G.D.), Savin 2207 (very old). E. Anterior view, same specimen.

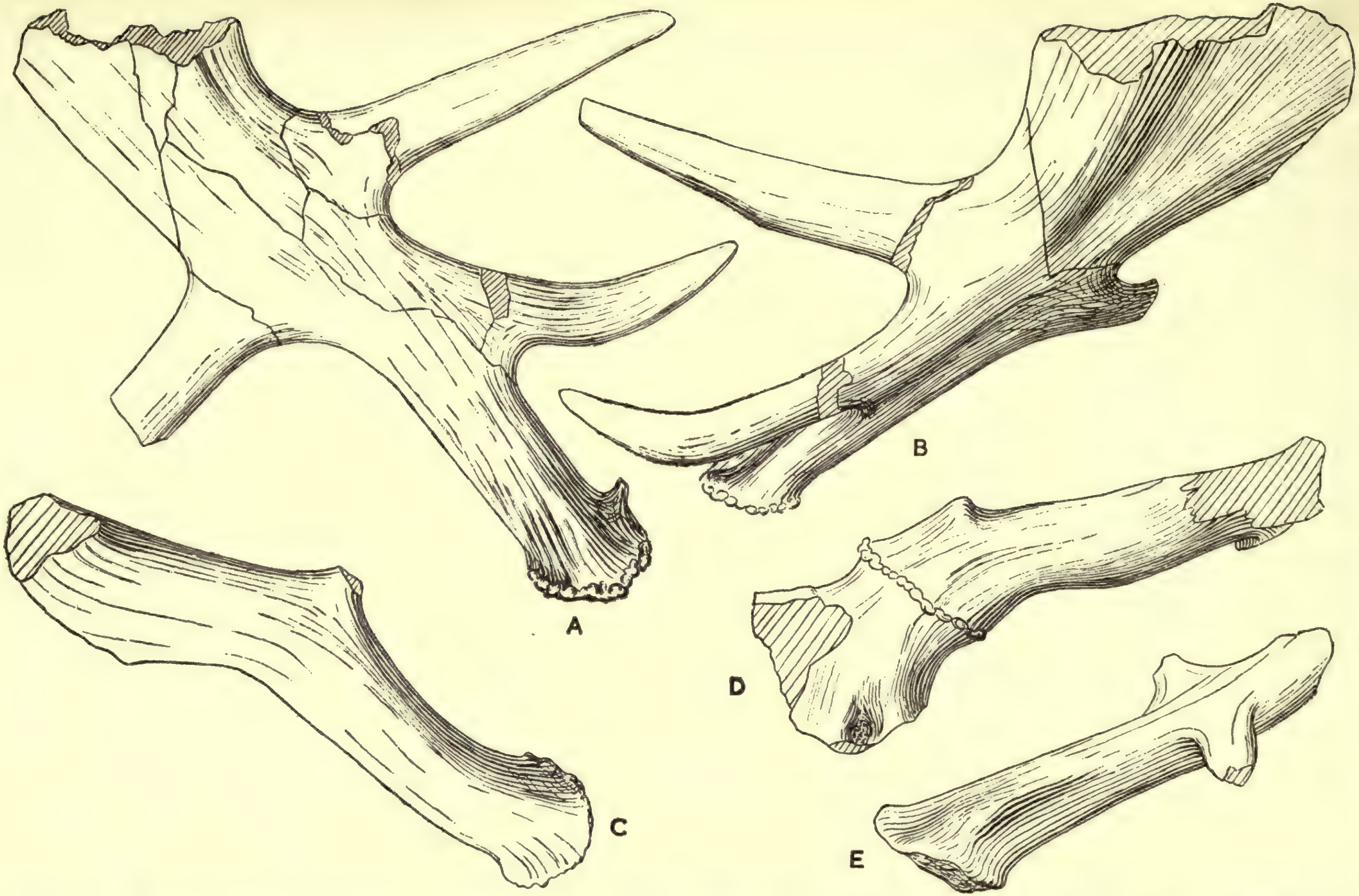

FIG. 34. *Megaceros dawkinsi*, antlers. ¼ natural size. A. Mundesley, B.M. (G.D.), Savin 1720. Anterior view. B. The same specimen, oblique, posterior view. C. Mundesley, B.M. (G.D.), Savin 1291. D. Mundesley, B.M. (G.D.), Savin 2186. E. Bacton, B.M. (G.D.), Savin 1897.

of the molars, undergone by *Megaceros giganteus* and *M. mosbachensis*. Nor can the antlers be considered primitive. The pedicles are disproportionately strong for their size; moreover, in cross-section the beam is thinner than the pedicle and is

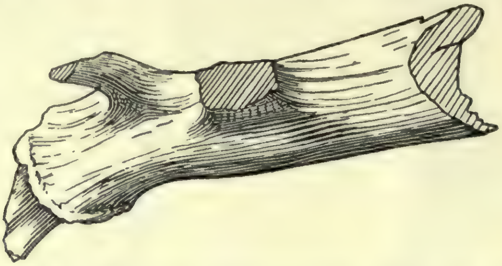

FIG. 35. *Megaceros dawkinsi*, left antler, seen obliquely from the outer side. Trimingham, B.M. (G.D.), Savin 1820. ⅓ natural size.

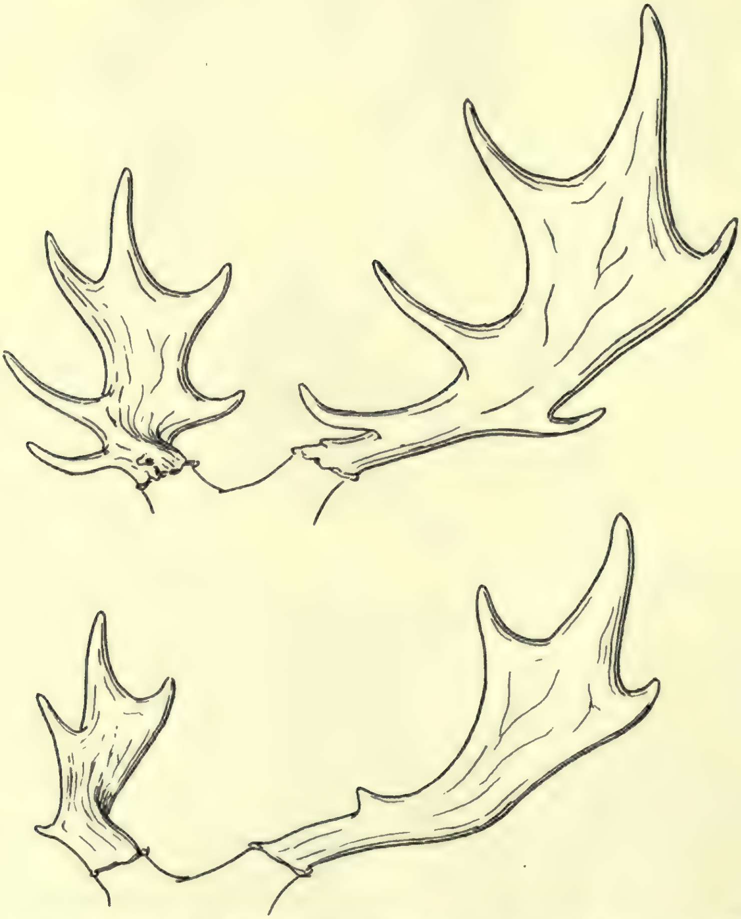

FIG. 36. *Megaceros dawkinsi*, reconstructions of the antlers based on the specimens of Figs. 33 & 34. ⅛ natural size.

stretched backwards—two common features in the deer with reduced antlers. The unusually high instability of the tines is also a character peculiar to regressed antlers.

Whether this regression of *M. dawkinsi* was due to inner factors or to influence of the environment can hardly be stated. The characters of the dentition suggest habits of life in open, grassy lands, rather than in woodlands; this is a rather unusual habitat for deer.

*Megaceros belgrandi* and several related forms from Central and Eastern Europe, listed above, are closely similar to *M. dawkinsi* and possibly identical with it, but their remains are very imperfect.

A striking similarity with the antlers of *M. dawkinsi* is shown by an antler of *Cervus cazioti* from the cave of Nonza in Corsica, figured by Depéret (1897*a*), which, however, is less than half the size of the antlers of *M. dawkinsi*. *Cervus cazioti* is no doubt a dwarf island form. Also its dentition recalls *M. dawkinsi*.

MEASUREMENTS:—

| Frontal | B.M. (G.D.) M. 6302 Sidestrand |
|---|---|
| Minimal breadth beneath the pedicles | 164 |

| Lower jaws | B.M. (G.D.), Savin 526 Overstrand | B.M. (G.D.), M. 6224 Sidestrand | B.M. (G.D.), Savin 339 Mundesley | B.M. (G.D.), Savin 533 Overstrand |
|---|---|---|---|---|
| Total length of the tooth row | 128 | 134 | 125 | 123 |
| Breadth of $M_2$ | 15 | 15 | 15 | 14, 5 |

## *Megaceros savini* (Dawkins)

(Figs. 23 D, 28 K, L, 29 C, D, 37–40.)

1887. *Cervus savini* Dawkins (pars), p. 11, pl. 3, fig. 3, 5 ?
1891. *Cervus savini* Dawkins: Gunn (pars), pl. 7, figs. 4, 5.
1891. *Cervus* sp. Gunn, pl. 4, fig. 101, pl. 6, fig. 2.
1891. *Cervus savini* Dawkins: Newton, p. 30.

SYNONYMY. Dawkins included in this species also an antler of *Euctenoceros ctenoides* (1887, pl. 3, fig. 4) and a fragment of a young specimen whose identity is uncertain (pl. 3, fig. 2), but Newton pointed out that these identifications are incorrect. Gunn attributed to it a frontal (pl. 4, fig. 102), which might possibly belong to a red deer.

OCCURRENCE. This species is fairly frequent and is represented by not less than twenty antlers in the British Museum and at Norwich. Eleven of them were found at Trimingham, the others at Sidestrand, Overstrand, Mundesley and Kessingland. A frontal from Kessingland (Figs. 23 D, 37) and possibly another frontal from Pakefield (Dawkins, 1887, pl. 3, fig. 5) represent all that is known of its skull.

The remains of dentition I tentatively refer to this species consist of three lower jaws from Trimingham and Mundesley, in the British Museum.

DESCRIPTION. The frontal, which indicates an animal of about the same size as *Megaceros verticornis*, clearly shows the hollowed forehead of the group of *Megaceros giganteus*. The identification of the frontal (Figs. 23 D, 37) is made possible by the basal portion of the antler.

The antlers include specimens of all ages. The type (Dawkins, 1887, pl. 3, fig. 3) is of medium size, but the largest specimens, represented by basal fragments (Fig. 38 A, and a more imperfect fragment in the Norwich Museum, from an unknown locality), attained the size of *Megaceros verticornis* and *M. giganteus*. The beam is flattened and hollowed below and bears a prominent ridge on its anterior side. The brow tine (Fig. 38 C, D, and Gunn, 1891, pl. 6, fig. 2) branches off close to the burr; it is flattened, broadly expanded into a small palmation, and set horizontally. It is very often broken off at the base, and I do not know any specimen where it is complete. The section of its base is triangular, with the longer side above. The antlers are widely divergent, as in *M. giganteus* and in *M. verticornis* (Fig. 39). The anterior and posterior tines are much flattened; above the posterior tine the beam is bent upwards, becomes still more flattened and branches into two terminal tines, apparently of equal size.

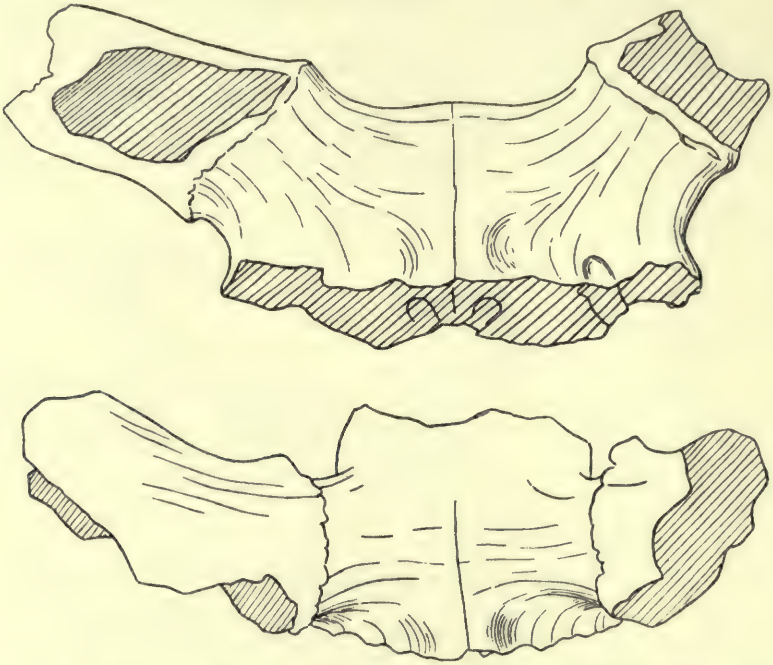

FIG. 37. *Megaceros savini*, frontal, Kessingland. Norwich Museum 321. (See also Fig. 23.) ½ natural size.

The teeth I tentatively refer to this species are intermediate in size between those of *M. verticornis* and those of *M. dawkinsi*. The distinction is not sharp, and in their extreme variations these species, especially *M. verticornis* and *M. savini*, may perhaps overlap. The lower tooth row is identical with that of *Megaceros dupuisi* (Stehlin, 1912). $P_4$ is primitive. The teeth I have seen are rather worn, but they do not seem to be hypsodont. The enamel is of medium thickness.

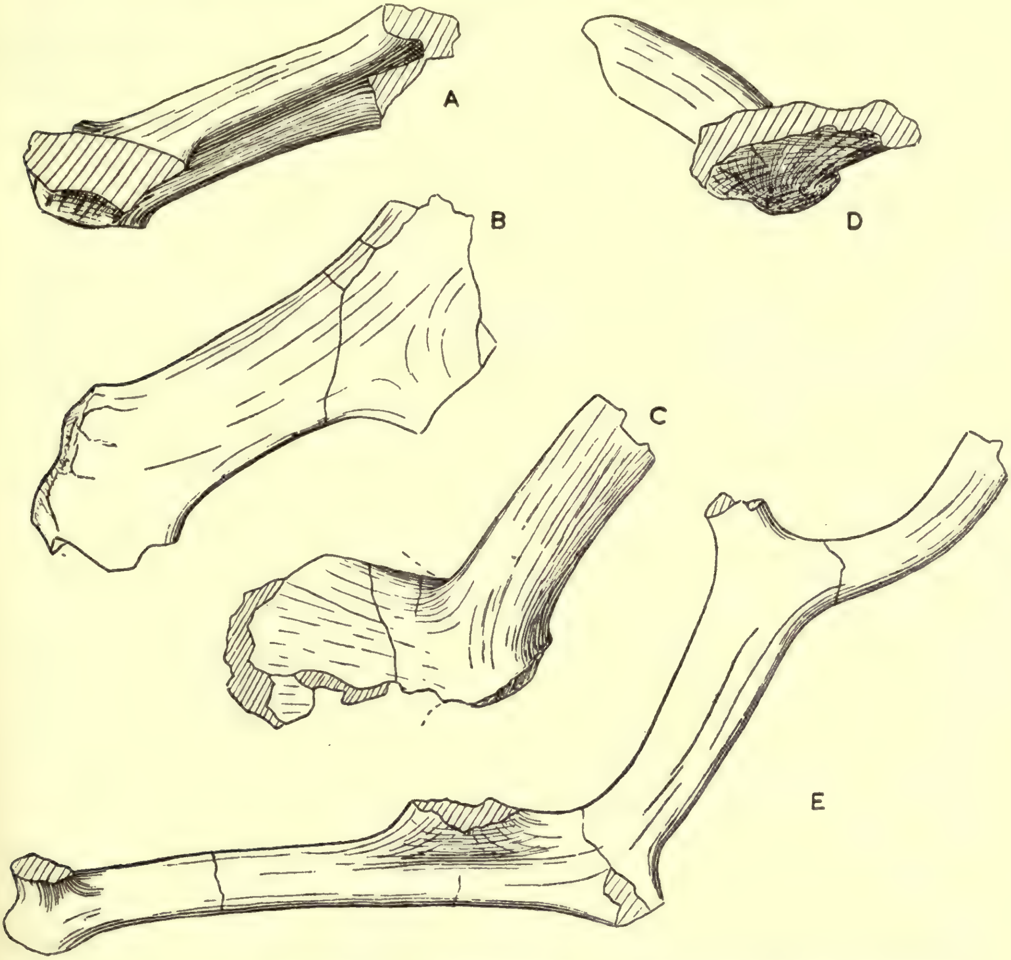

FIG. 38. *Megaceros savini*, antlers. ¼ natural size. A & B. Trimingham, large specimen. B.M. (G.D.), Savin 1422. C & D. Overstrand, medium sized specimen. B.M. (G.D.), Savin 1880. E. Trimingham, young specimen. B.M. (G.D.), Savin 1241.

Two imperfect maxillae from Trimingham might perhaps belong to this species.

MEASUREMENTS:—

| Lower jaw: | B.M. (G.D.), M. 6220<br>Trimingham |
|---|---|
| Total length . . . | 135 |
| Breadth of $M_2$ . . | 16 |

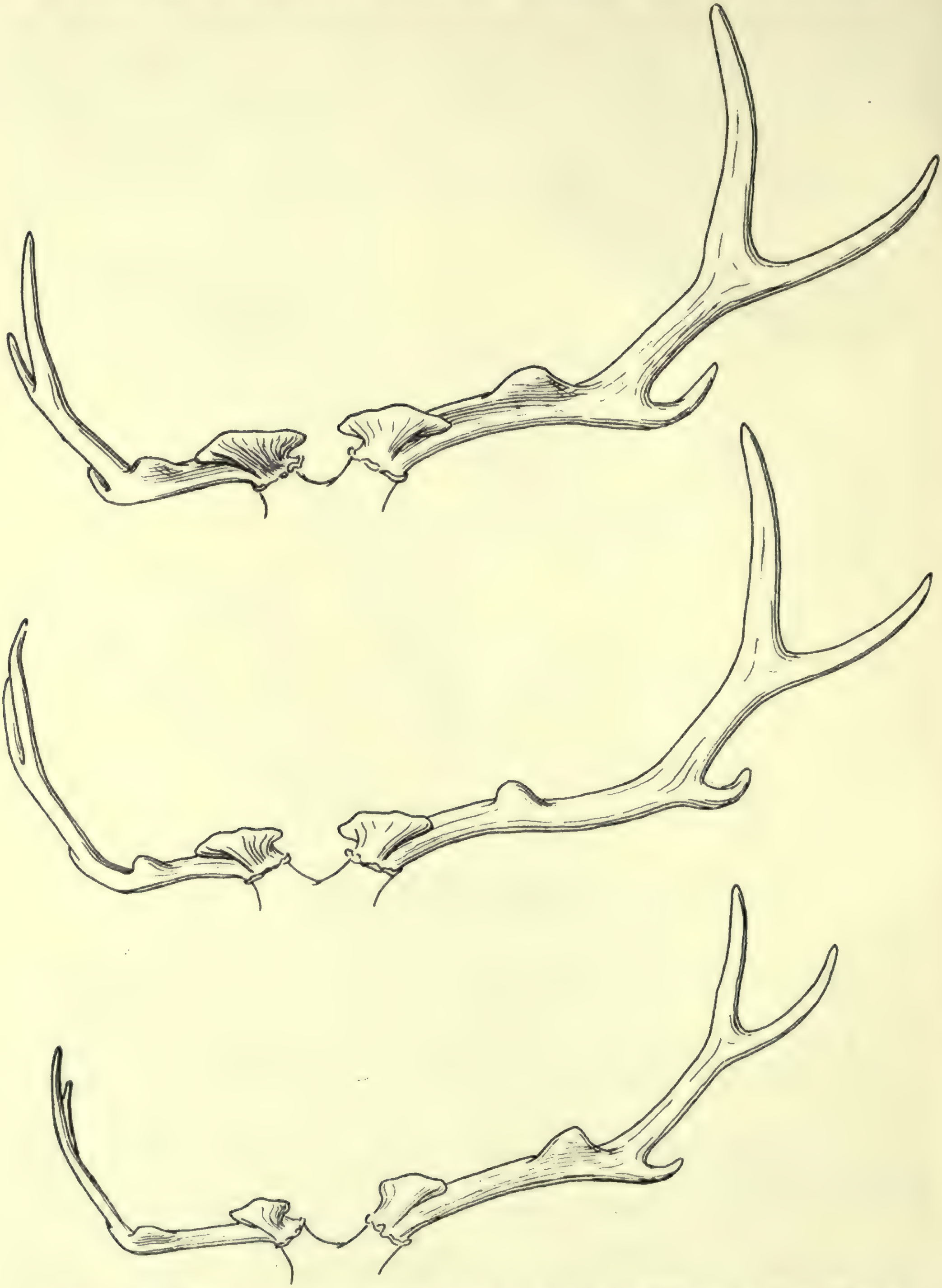

FIG. 39. *Megaceros savini*, reconstruction of the holotype, B.M. (G.D.), M. 6093, and of the specimens of Fig. 38. $\frac{1}{10}$ natural size.

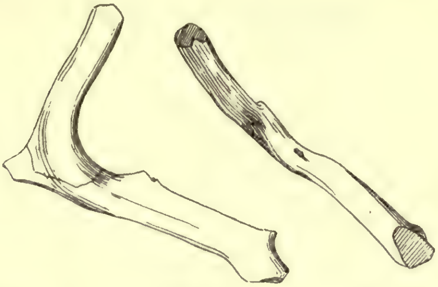

FIG. 40. *Megaceros savini ?* Very young specimen. Bacton, B.M. (G.D.), Savin 910. $\frac{1}{5}$ natural size.

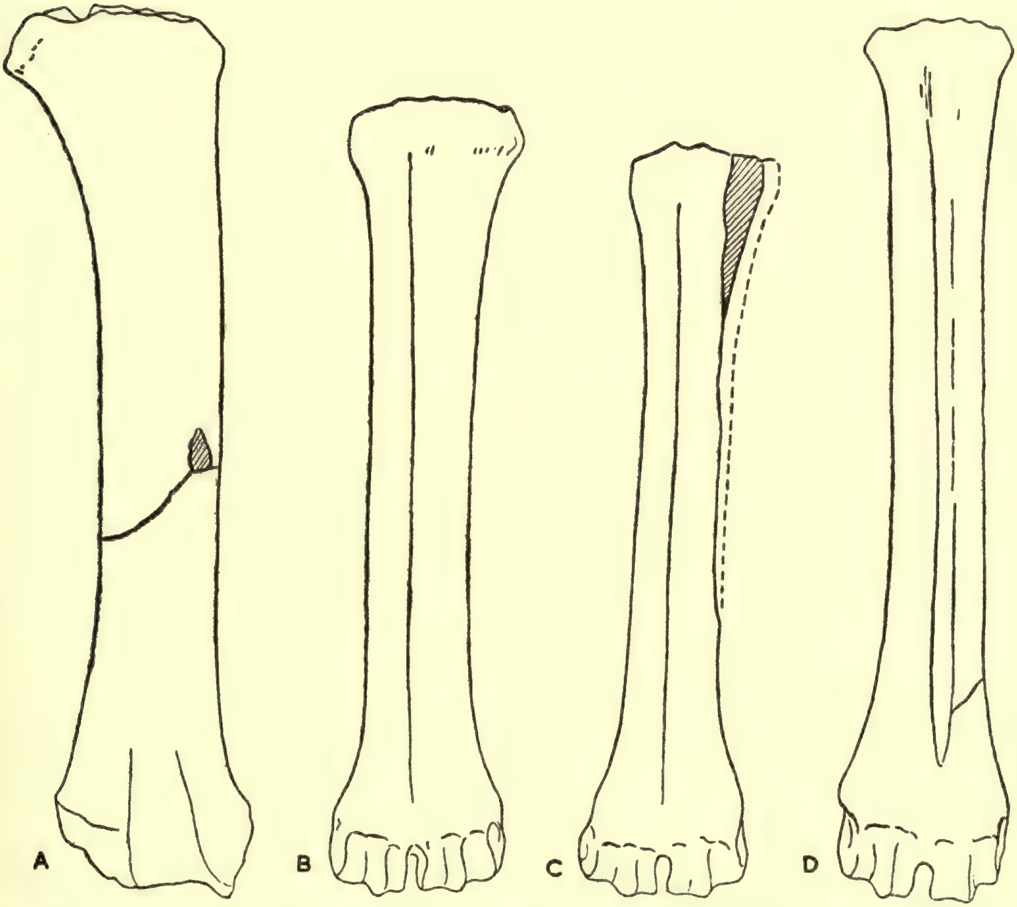

FIG. 41. *Megaceros*, limb bones. $\frac{1}{3}$ natural size. A. *M. verticornis* or *savini*. Right radius. No locality, B.M. (G.D.), Savin 1462. B. *M. verticornis* or *savini*. Right metacarpal, Trimingham. B.M. (G.D.), Savin 1104. C. *M. dawkinsi ?* Right metacarpal, Mundesley. B.M. (G.D.), Savin 2024. D. *M. verticornis* or *savini*, Left metapodial, Trimingham. B.M. (G.D.), Savin 1450.

### ***Megaceros* incertae sedis**

(Fig. 41 A–D.)

LIMB BONES. Fourteen complete limb bones may be attributed to the genus *Megaceros* for their large size and heavy form. They are: two radii, three metacarpals and four metatarsals in the British Museum; a metacarpal and a tibia in the Norwich Museum; a radius, a metacarpal and a metatarsal in the Museum of the Geological Survey. The metapodials are characterized by the broad form of their distal articulations and are easily recognizable.

The larger bones are of the same size as *Megaceros giganteus* and may be attributed to *M. verticornis* or to *M. savini*; the smaller ones probably belong to *M. dawkinsi*, or to females of the larger species.

MEASUREMENTS:—

| Radius : | B.M. (G.D.), Savin 464. Trimingham | B.M. (G.D.), Savin 1462. (No locality) | G.S. 21688. Kessingland |
|---|---|---|---|
| Total length | 340 | 349 | 320 |
| Proximal breadth | 79 | 82 | — |
| Distal breadth | — | 73 | — |

| Metacarpal : | B.M. (G.D.), Savin 1104. Trimingham | B.M. (G.D.), Savin 376. Sidestrand | B.M. (G.D.), Savin 2024. Mundesley |
|---|---|---|---|
| Total length | 304 | 293 | 286 |
| Proximal breadth | 64 | 56 | — |
| Distal breadth | 68 | 60 | 63 |

| | G.S. TF/55. Mundesley | Norwich Museum 531. (No locality) | B.M. (G.D.), Savin 1885. Sidestrand |
|---|---|---|---|
| Total length | 271 | 310 | 261 |
| Proximal breadth | 51 | 70 | 48 |
| Distal breadth | 58 | 74 | 52 |

| Tibia : | Norwich Museum 526. (No locality) |
|---|---|
| Total length | 482 |
| Distal breadth | 81 |

| Metatarsal : | G.S. 21684. Kessingland | B.M. (G.D.), M. 6491. Trimingham | B.M. (G.D.), Savin 1450. Trimingham |
|---|---|---|---|
| Total length | 348 | 358 | 345 |
| Proximal breadth | 57 | 59 | 55 |
| Distal breadth | 65 | 67 | 64 |

## CERVIDAE *incertae sedis*

### " *Cervus* " *obscurus* n. sp.

(Figs. 42–45.)

SYNTYPES. B.M. (G.D.), Savin 195, Mundesley (Fig. 42 A, B); B.M. (G.D.), M. 2321, Forest Bed : no exact locality (Fig. 42 C–E) ; B.M. (G.D.), M. 6421, Overstrand (Fig. 43).

ADDITIONAL SPECIMENS. Two lower portions of shed antlers and three basal fragments of antlers with the frontals; two of these (Fig. 44 C, D) possibly belong to the same individual.

OCCURRENCE. Bacton, Mundesley, Sidestrand and Overstrand. In addition, an antler of doubtful attribution from Trimingham.

DIAGNOSIS. A cervid of large size characterized by a small lower basal tine directed downwards, a large upper basal tine strongly twisted outwards, a massive beam and an upper tine set far apart from the basal tines.

DESCRIPTION. This is a species of very unusual features. The size is large and the forms are massive as in *Euctenoceros dicranios* and *ctenoides*. The forehead is marked by a prominent median suture and two shallow ridges along the inner borders of the pedicles, as in *Megaceros verticornis* and its relatives, but is narrower. A small tine is given off close to the burr, at a wide angle with the beam, and is inclined inwards and downwards. A second basal tine, much more robust, arises at some distance from the burr and is strongly bent outwards. It is rather long and is flattened at its end. The beam is massive, straight, and ovoidal in cross-section, with the major axis set vertically. A third tine, directed upwards, is given off at a very great distance from the burr. The grooves of the blood-vessels are shallow.

The remaining parts of the frontals enable one to reconstruct the position of the antlers. The beams diverge at about 45° from the median plane of the body.

The antler from Trimingham which I doubtfully identify with this species (Fig. 44 A, B) differs in the characters of the lower tines. The lower tine arises at some distance from the burr; a second tine arises from the inner side, near its base. This tine corresponds for its position to the small knob between the two basal tines of the syntype of Fig. 42 C, D, E.

AFFINITIES. The systematic position of this species is quite uncertain. No doubt it does not belong to the genus *Cervus* in the restricted sense defined in the previous pages. The lower portion of the antlers recalls that of *Megaceros verticornis*, but the characters of the upper portion of the antlers and of the forehead rule out any relationship with *Megaceros*; they rather point to some affinity with *Euctenoceros*, but this question is still open.

### *Specimens of Doubtful Attribution*

LOWER JAWS. Two lower jaws from Overstrand and Trimingham (Figs. 28 J, 46, 47) might belong either to " *Cervus* " *obscurus* or to *Euctenoceros sedgwicki*. They both belong to young but fully grown specimens. The teeth are massive and

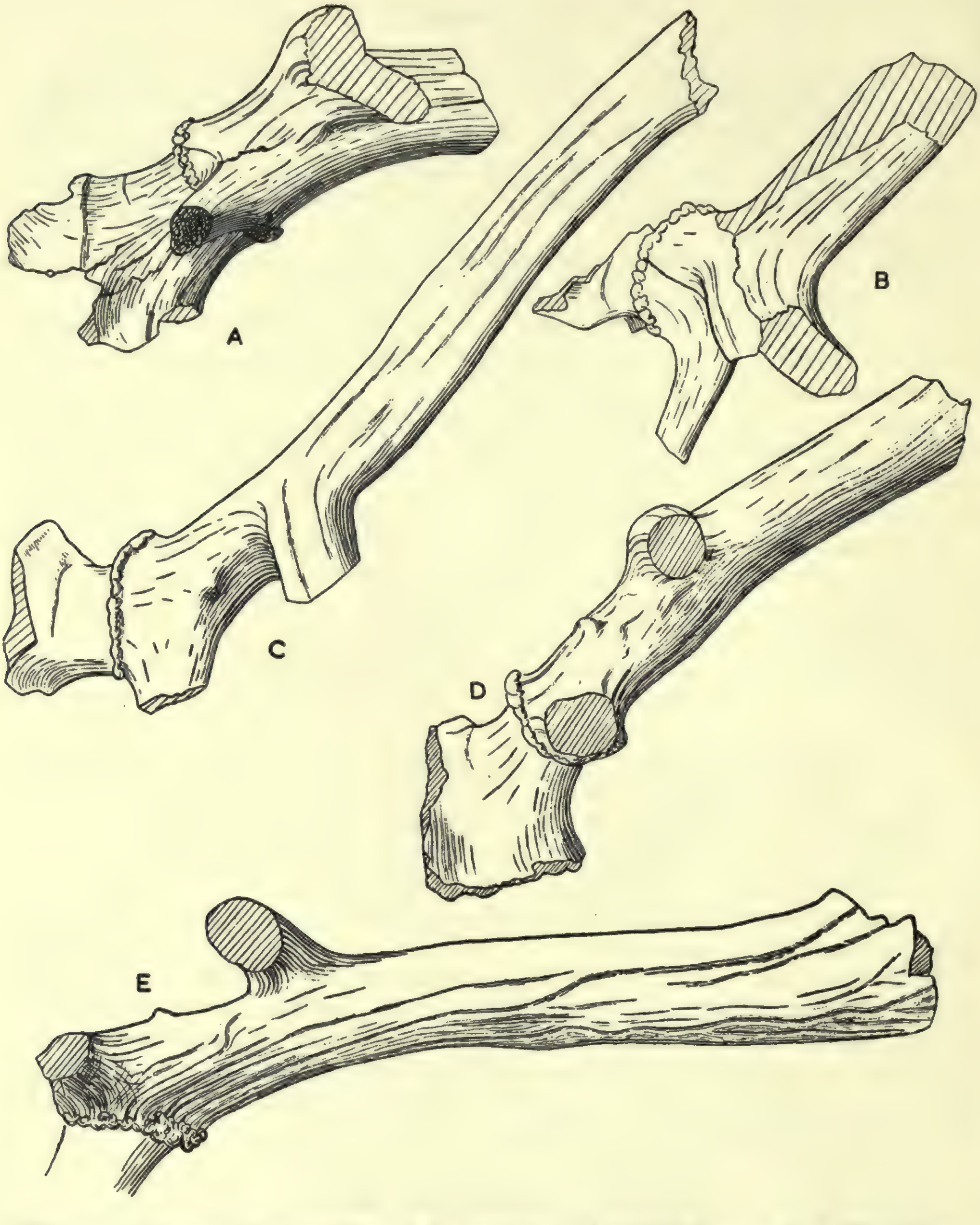

Fig. 42. "*Cervus*" *obscurus*, two of the syntypes. ¼ natural size. A & B. Mundesley, B.M. (G.D.), Savin 195. C, D & E. Forest Bed, B.M. (G.D.), M. 2321.

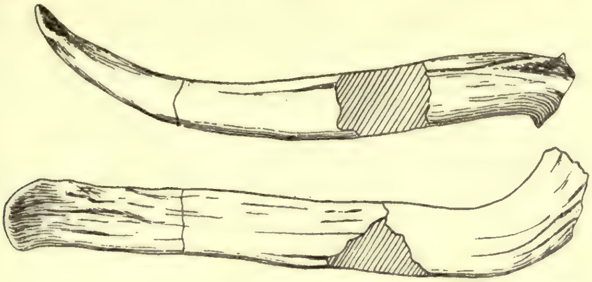

FIG. 43. "*Cervus*" *obscurus*. Syntype, Overstrand. B.M. (G.D.), M. 6421. ¼ natural size.

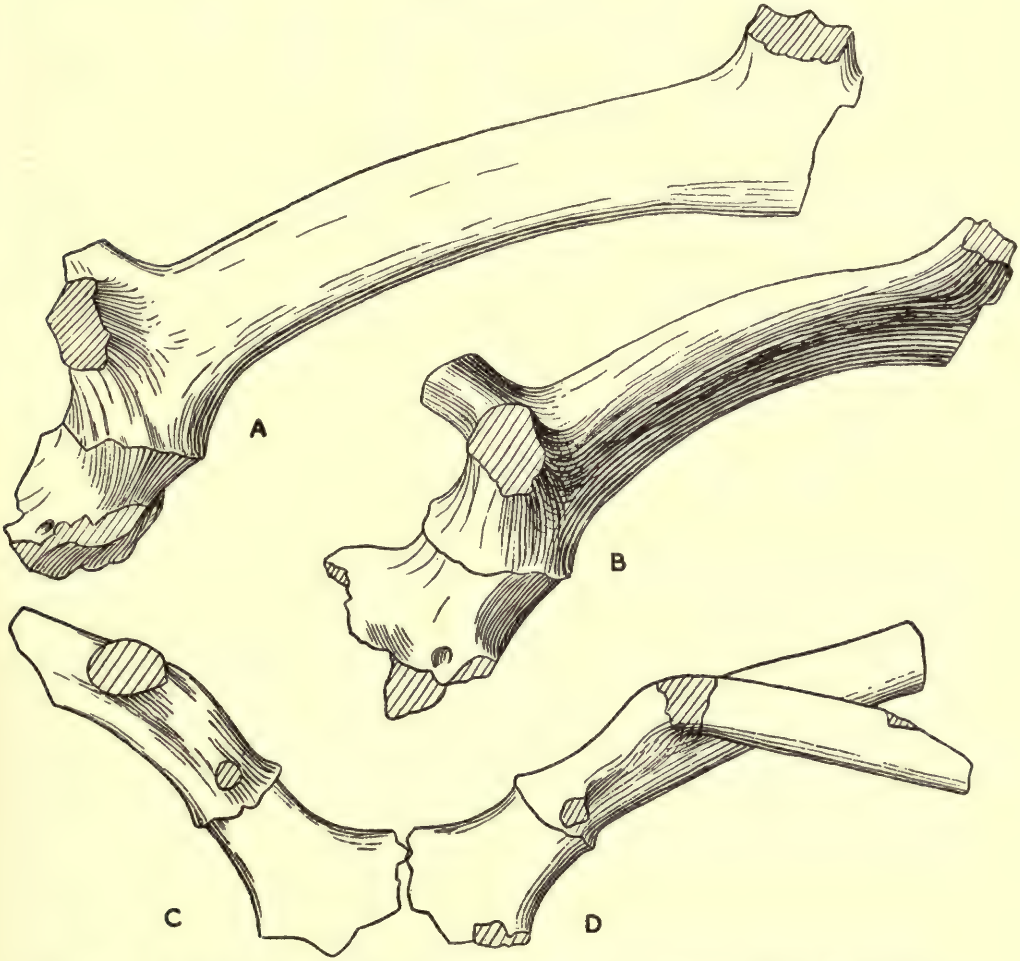

FIG. 44. A & B. "*Cervus*" *cf. obscurus*, Trimingham. B.M. (G.D.), M. 6400. C. "*Cervus*" *obscurus*, right antler of young specimen, Mundesley. B.M. (G.D.), M. 6307. D. "*Cervus*" *obscurus*, left antler of a young specimen, Mundesley. B.M. (G.D.), M. 6315, probably both belonging to the same individual. ¼ natural size.

seem to be slightly more hypsodont than those from East Runton which I tentatively refer to *Euctenoceros ctenoides*. $P_4$ has a complete internal wall and the molars bear a strong anterior ridge. The ramus is depressed and thick, and its cross-section closely resembles that of the lower jaws of *Euctenoceros* from the Upper Valdarno (Azzaroli, 1948, fig. 11, no. 3). The jaw from Trimingham, which is more complete, is distinguished by a large coronoidal process. The breadth of $M_2$ is 17 mm.

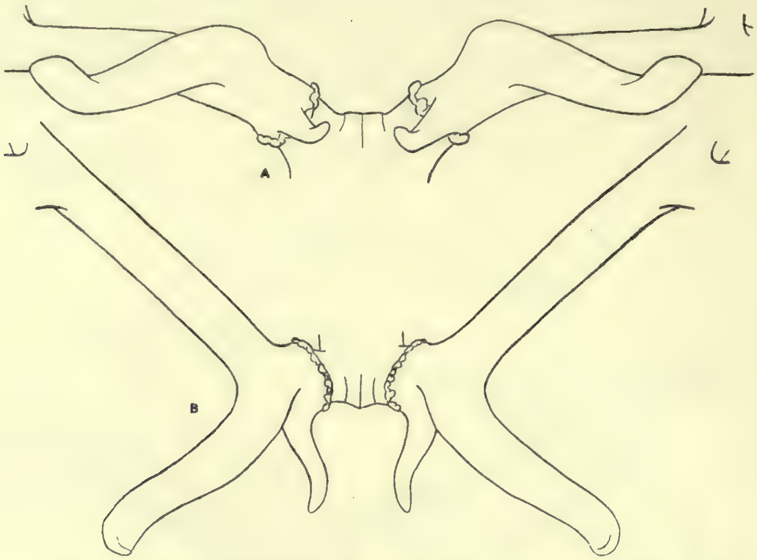

FIG. 45. " *Cervus* " *obscurus*, tentative reconstruction, based on the syntypes. $\frac{1}{8}$ natural size. A. Anterior view. B. Dorsal view.

BRAIN CASE. The identification of a brain case from Trimingham (B.M. (G.D.), M. 6303) is uncertain. The shortness of the pedicles gives evidence that it belonged to a fully grown specimen; they are, however, too small for *Euctenoceros ctenoides*, *E. sedgwicki* or " *Cervus* " *obscurus*. Moreover, the forehead is hollowed, and bears no trace of the ridges which distinguish the latter species. *Euctenoceros tetraceros* is not recorded at Trimingham, and the supraoccipital crest of the specimen in question is much stronger than that of the skull roof from East Runton I tentatively identify with *E. tetraceros*. The brain case from Trimingham might possibly belong to *Cervus* cf. *elaphus*; however, it exceeds the size even of the largest specimens from Val di Chiana (Azzaroli, 1948).

MEASUREMENTS:—

| | |
|---|---|
| Occipital breadth . . . . . . . | 156 |
| Occipital height . . . . . . . | 93 |
| Minimal frontal breadth . . . . . . | 152 |
| Breadth of the brain case between the parietals . | 104 |
| Breadth of the condyles . . . . . . | 89 |

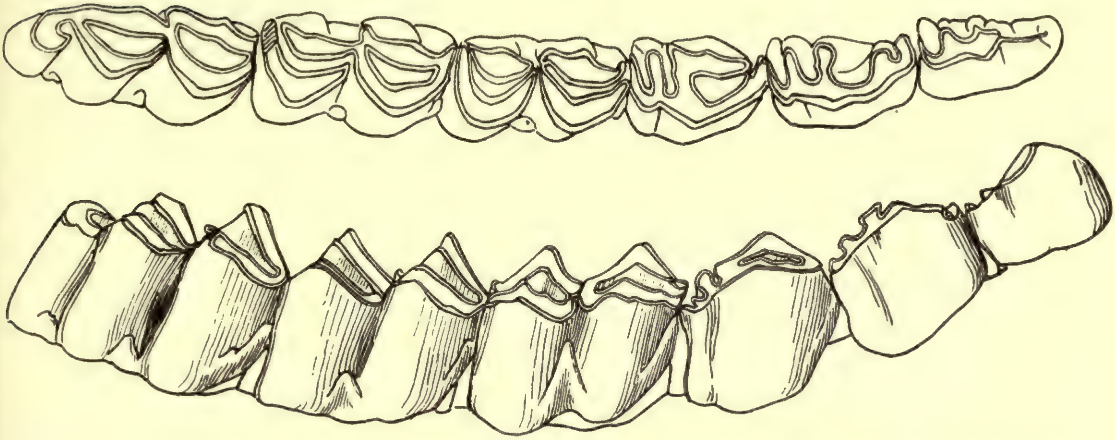

FIG. 46. Cervid indet., lower dentition. Trimingham, Norwich Museum 45. Natural size.

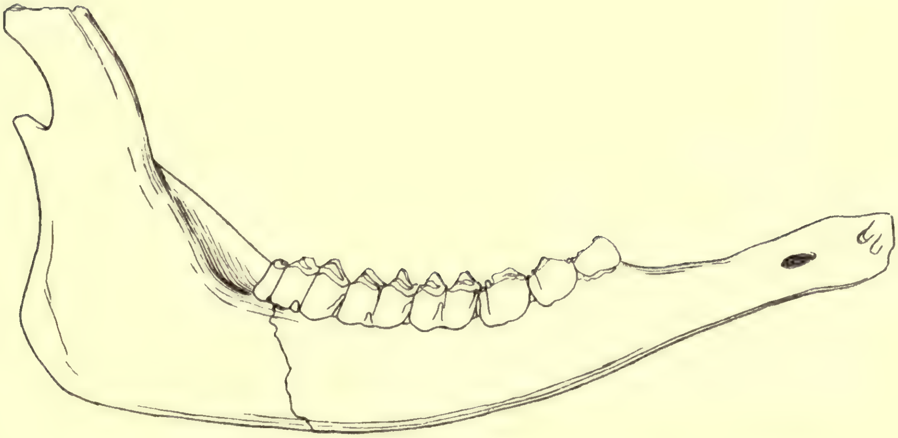

FIG. 47. Cervid indet., Trimingham, Norwich Museum 45. (See also Fig. 46.) ⅓ natural size.

LIMB BONES. An account of the complete limb bones is given in the following table of measurements; some of them have been reproduced in Fig. 48. The metapodials are easily recognizable from those of *Megaceros* by the narrower form of their distal articulation, but a more precise determination is difficult and can be based only on the proportions. They might be attributed to *Euctenoceros*, to the red deer, or to " *Cervus* " *obscurus*.

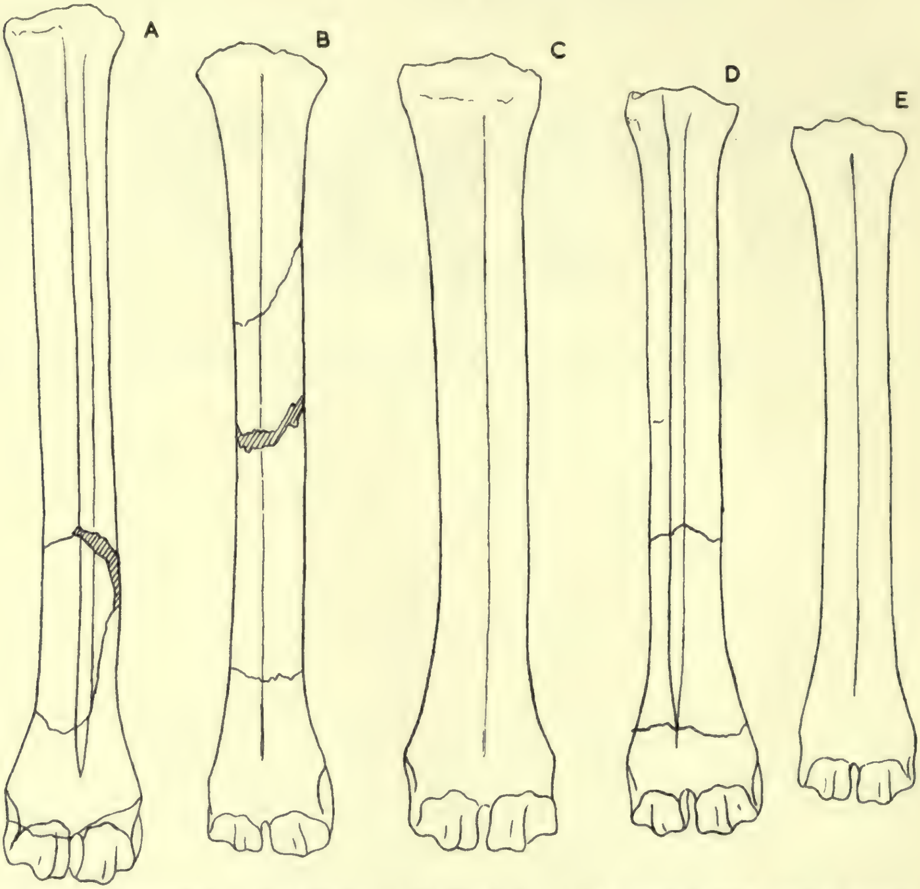

FIG. 48. Cervids indet., limb bones. ⅓ natural size. A. Left metatarsal, West Runton, Upper Freshwater Bed. B.M. (G.D.), Savin 1643. B. Left metacarpal, Trimingham. B.M. (G.D.), Savin 2168. C. Left metacarpal, Trimingham. B.M. (G.D.), M. 6473. D. Right metatarsal, Overstrand. B.M. (G.D.), Savin 773. E. Right metacarpal, East Runton. B.M. (G.D.), M. 6476.

Some bones from Trimingham and from West Runton (B.M. (G.D.), Savin 2168, 1424, 1643) are long and slender like those of *Libralces gallicus*, but their shape is quite different and leaves little doubt that they belong to a cervine. Their identification is puzzling; *Euctenoceros ctenoides* and *E. tetraceros* can be excluded, and an identity with the red deer seems extremely improbable, although only this among the five species quoted above has been found in the Upper Freshwater Bed at West Runton. *Euctenoceros sedgwicki* was presumably as heavy an animal as the largest representatives of its genus. An identification with "*Cervus*" *obscurus* seems less improbable.

MEASUREMENTS:—

| Radius: | B.M. (G.D.), 1105. Trimingham | B.M. (G.D.), M. 6469. Sidestrand |
|---|---|---|
| Total length | 337 | 325 |
| Proximal breadth | 70 | — |
| Distal breadth | 63 | 61 |

| Metacarpal: | B.M. (G.D.), Savin 2168. Trimingham | B.M. (G.D.), Savin 1424. Trimingham | B.M. (G.D.), M. 6476. East Runton | | B.M. (G.D.), M. 6473. Trimingham | |
|---|---|---|---|---|---|---|
| Total length | 321 | 316 | 267 | 283 | 306 | 291 |
| Proximal breadth | 51 | 53 | 45 | 50 | 55 | 52 |
| Distal breadth | 50 | 53 | 45 | 50 | 57 | 53 |

| Femur: | B.M. (G.D.), Savin 1446. Trimingham |
|---|---|
| Total length | 360 |
| Proximal breadth | 103 |
| Antero-posterior diameter of the distal epiphysis | 85 |

| Metatarsal: | B.M. (G.D.), Savin 1685. Trimingham | B.M. (G.D.), Savin 1071. Overstrand | B.M. (G.D.), Savin 773. Overstrand | B.M. (G.D.), M. 6490. Sidestrand |
|---|---|---|---|---|
| Total length | 310 | 307 | 311 | 265 |
| Proximal breadth | 42 | 41 | 45 | 39 |
| Distal breadth | — | 47 | 52 | — |

| | B.M. (G.D.), M. 6495. East Runton | | B.M. (G.D.), Savin 1643. West Runton, U. Freshw. Bed |
|---|---|---|---|
| Total length | 293 | 293 | 347 |
| Proximal breadth | 44 | 41 | 46 |
| Distal breadth | 50 | 47 | 54 |

## Cervid cf. ***Dama nestii nestii***

(Fig. 49.)

1882. *Cervus etueriarum* ? Croizet & Jobert: Newton, p. 55.
? 1889. *Cervus rectus* Newton, p. 145, fig. 1, 1*a*.
? 1891. *Cervus rectus* Newton: Newton, p. 30, pl. 4, fig. 1.

SYNONYMY. Newton's *Cervus rectus* is based on a very young specimen, probably of this species, as may be seen by comparison of the type with fig. 1 n° 1, 2 in Azzaroli, 1948.

OCCURRENCE. Seven lower portions of antlers and a fragment of the upper portion, from East Runton; two basal fragments from Sidestrand and one from

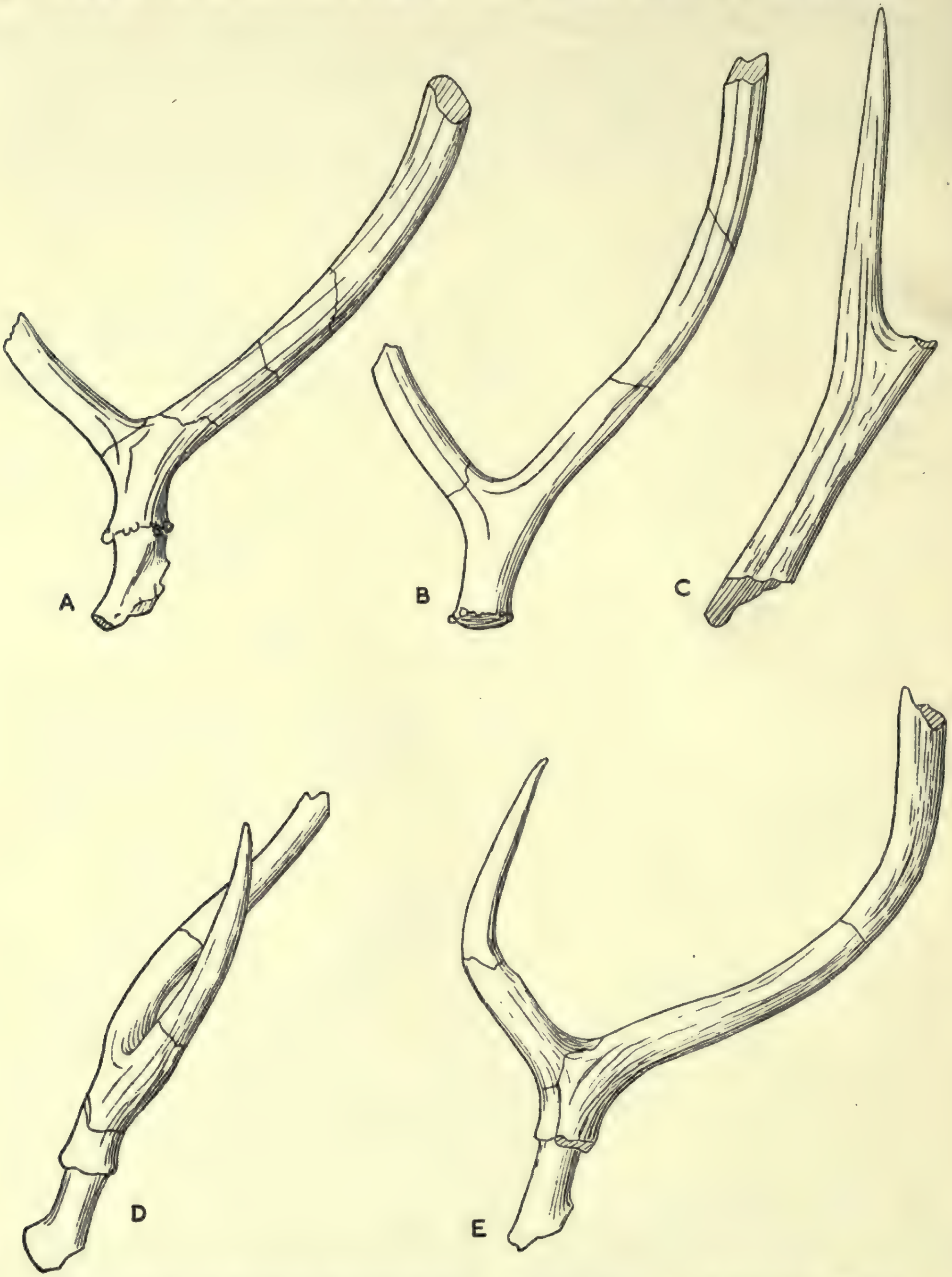

FIG. 49. Cervid cf. *Dama nestii nestii*, antlers. ¼ natural size. A. Left antler, Mundesley. B.M. (G.D.), Savin 1164. B. Left antler, East Runton. B.M. (G.D.), M. 6365. C. Fragment of the upper portion of a left antler, East Runton. B.M. (G.D.), M. 6389. D & E. Left antler, East Runton. B.M. (G.D.), M. 6568.

Mundesley. Probably two isolated $M_3$ and some imperfect metapodials from East Runton.

Description and comparisons. This species is poorly represented. The antlers correspond with those of *Dama nestii nestii* from the Upper Valdarno and Olivola (Azzaroli, 1948) for the position and development of the brow tine and the regular helicoidal torsion of the beam. Also the fragment of the upper portion agrees with the terminal fork of this subspecies; the curvature of the beam and the characters of the fork give evidence that the bifurcation took place in a transverse plane. If so, the antler had four tines.

The other species with which this species can be compared are: *Cervus philisi* from Sénèze (Schaub, 1942), *Cervus rhenanus* from Tegelen (Hooijer, 1947) and *Cervus perolensis* from the Auvergne (Bout & Azzaroli, 1953). *Cervus philisi* differs in the stronger development of the brow tine, the straighter form of the beam, and the characters of the upper portion of the antlers. *Cervus rhenanus*, whose antlers are more imperfectly known, differs mainly in the higher position of the brow tine, and *Cervus perolensis*, also imperfectly known, in the stronger development of the brow tine. These three species are rather primitive and their relationships are not yet clear.

### Cervid cf. ***Dama clactoniana*** Falc.

(Fig. 50)

I include here several specimens of the size of a fallow deer. Their identification is somewhat uncertain and they might possibly include more than one species. Their age is also uncertain, but at least the specimens from the Upper Freshwater Bed are certainly post-Villafranchian.

Antlers (Fig. 50). Three basal fragments from Bacton, Trimingham, and West Runton (Upper Freshwater Bed). They are distinguished by a very stout basal bifurcation and a strong curvature of the brow tine. The pedicles are small. The antlers from Bacton and from West Runton are disproportionately large for their pedicles and probably belong to old individuals.

Teeth. Several isolated teeth and a complete lower tooth row from the Upper Freshwater Bed at West Runton; two imperfect lower jaws, from Overstrand and Trimingham. The lower molars bear well-developed basal columns. The $P_4$ from Overstrand is primitive, two $P_4$ from West Runton are advanced. The total length of the lower tooth row from West Runton is 100 mm.

Limb bones. Two perfect metacarpals, from Overstrand and Trimingham. Fragments of about the same size occur in the Upper Freshwater Bed of West Runton.

Measurements:—

| Metacarpal | B.M. (G.D.), M. 6475. Overstrand | B.M. (G.D.), Savin 1399. Trimingham |
|---|---|---|
| Total length | 232 | 235 |
| Proximal breadth | 35 | 35 |
| Distal breadth | 35 | 35 |

Comparisons. In the Villafranchian fauna only *Dama nestii eurygonos* (Azzaroli, 1948) can be compared with the above specimens. However, the specimens from Bacton and West Runton are larger than this subspecies; moreover those from West Runton are certainly younger, and this is probably true also for those from Bacton and Trimingham. After the close of the Villafranchian, no deer of this size is known until the Clacton stage.

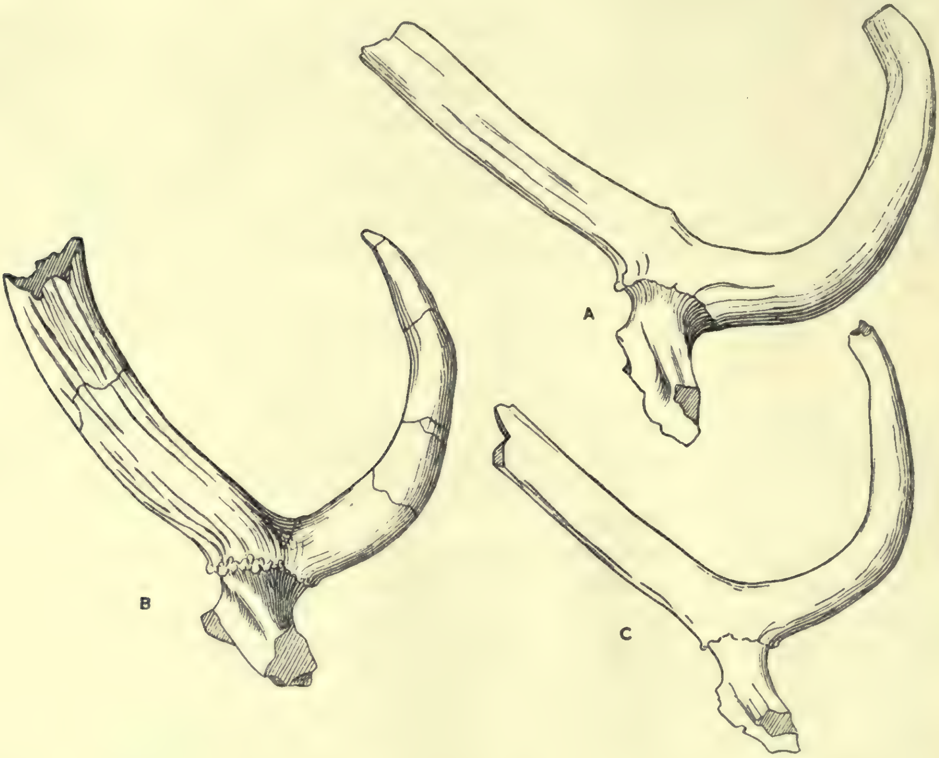

Fig. 50. Cervid cf. *Dama clactoniana*, right antlers. ¼ natural size. a. Abnormal specimen, Bacton, very old? B.M. (G.D.), Savin 1283. b. Abnormal specimen, very old? West Runton, Upper Freshwater Bed. B.M. (G.D.), Savin 554. c. Trimingham, B.M. (G.D.), M. 6367.

In this horizon we find in East Anglia *Dama clactoniana* (Bate, 1938, Oakley & Leakey, 1938), with which the fragments described above may be identified.

Keilhack (1888) described a pair of antlers of a large fallow deer from Belzig, near Berlin, which he supposed to belong to the Lower Pleistocene or even to the preglacial. But the occurrence of *Alces* in the same deposit points to an Upper Pleistocene age.

## Species incorrectly recorded from the Forest Bed

### " *Cervus* " *polignacus* Robert

1882. *Cervus polignacus* Robert: Newton, p. 59.
1891. *Cervus polignacus* Robert: Gunn, pl. 1, fig. 94, pl. 2, fig. 95.
1891. *Cervus polignacus* Robert: Newton, p. 29, pl. 4, fig. 12.

Newton, on Falconer's authority, referred to *Cervus polignacus* two imperfect antlers characterized by a low brow tine, branching at a very wide angle from the beam. These two specimens have been figured by Gunn and are now in the Norwich Museum. Several more imperfect antlers in the same museum have been referred to this species, and in the British Museum I have seen other fragments of a similar type. One of them, of a rather small size, has been incorrectly identified with *Megaceros savini* by Dawkins (1887, pl. 3, fig. 2). All these fragments are very unsatisfactory and are susceptible of different interpretations.

The name *Cervus Dama polignacus* was given by Robert (1829) to two incomplete skeletons from Solilhac: one of them is identical with his *Cervus solilhacus* (now *Megaceros solilhacus*) from the same locality. The second is a small red deer with abnormal characters; Pomel (1853) named it *Cervus roberti.*

### " *Cervus* " *carnutorum* Laugel

A fragment said to come from the Chillesford Clay at Aldeby, identified with *Cervus carnutorum* and figured by Dawkins (1872), may either belong to a large specimen of *Euctenoceros falconeri*, or to *E. sedgwicki.* Three specimens from the Norwich Crag quoted by Newton (1891, p. 26, pl. 4, fig. 3) possibly belong to *E. falconeri.* Other specimens from the Forest Bed determined as *Cervus carnutorum* in the collections belong to *E. sedgwicki.*

The name *carnutorum*, like *polignacus*, should be dropped (Stehlin, 1912).

### *Alces alces* L.

1891. *Alces ?* Gunn, pl. 6, fig. 4.

A much rolled antler of *Alces alces*, from an unknown locality, has been figured by Gunn. Its fossilization is less advanced than that of the other specimens, and no doubt it came from a younger horizon.

### *Megaceros giganteus* Blumenbach

1882. *? Cervus megaceros* Hart: Newton, p. 58.

Although this species was recorded from the Forest Bed by the earlier authors, Newton excluded it.

An isolated $P_4$ from Sidestrand, in the Savin collection, registered B.M. (G.D.), Savin 1601, might possibly belong to this species, but its occurrence in the Forest Bed can be excluded.

### *Rangifer tarandus* L.

1891. *Cervus* sp. Gunn, pl. 6, fig. 3.

A much-rolled fragment of an antler, found on the beach at Pakefield, belongs to this species. Gunn questioned whether it belonged to the Forest Bed Fauna, and it can be excluded.

## CHRONOLOGY

### *The Characters of the so-called Forest Bed Fauna*

The so-called Forest Bed Fauna is very abundant in species, and includes representatives of faunas met with at different horizons in continental Europe. This unusual assemblage has been explained in various ways. Whereas the older authors favoured an Upper Pliocene age (Reid, 1890, with bibliography), or assumed that this fauna was partially or totally derived (Dubois, 1905), more recent authors (Osborn, 1922, followed by Zeuner, 1945) attributed the whole fauna to the early Pleistocene (post-Villafranchian), and interpreted the archaic species as relics. Zeuner distinguished a " Cromer Forest Bed," where these archaic representatives are found, and a " Bacton Forest Bed " without archaic elements, which he thought to be a little younger.

All these interpretations are untenable. A Pliocene age is ruled out by the presence of species which immigrated into Europe after the close of Villafranchian times. On the other hand, the older representatives, once attributed to the Pliocene but actually of Upper Villafranchian age, do not constitute isolated relics; an entire faunal assemblage characteristic of that period is present. Moreover, primitive species occur together with their more advanced descendants, and Zeuner's " Cromer Forest Bed " is richer in species than any other locality. The deer, according to the present revision, include 15 species, and we cannot imagine that they lived at the same time. A derived fauna can also be excluded, as the fossils consist for a large part of large antlers of deer, jaws and limb-bones of elephants, all of them heavy and brittle, but rather well preserved. This is true both for the older and for the younger representatives of the fauna.

The alternative solution, namely, that the deposit includes several horizons, has been discussed in a previous section (" Geology "), and affords the only satisfactory explanation of the mixed character of the " Forest Bed Fauna." An attempt will be made here to determine the stratigraphical range of the 15 species of deer. It will be useful, however, first to illustrate the time scale we shall use for comparison.

### *Faunal changes during the Lower and Middle Pleistocene*

The Pleistocene continental sequence is marked by widespread faunal changes, consisting of extinctions of old forms, immigrations of new forms and evolution of primitive species into more advanced ones *in situ*.

Following the resolution made by the International Geological Congress in London (1948), we shall place the Calabrian, and its continental equivalent, the Villafranchian, at the base of the Pleistocene. However, it is now generally realized that the so-called main Villafranchian fauna does not constitute such a uniform assemblage as former authors assumed, and that it ranges over a relatively long lapse of time.

The well known faunas of the pumiceous sands and conglomerates of the Montagne de Perrier in Auvergne (Ravin des Etouaires, Roca Neyra, Pardines) are older than any of the other faunas hitherto attributed to the Villafranchian, and their inclusion in this stage is misleading. These faunas are broadly contemporaneous with those of the Roussillon (Depéret, 1897) and of the first lacustrine phase of the Upper Valdarno (lignites with *Tapirus arvernensis* and laminated clays with plants; see Merla, 1949 : 51–57). In the Montagne de Perrier two horizons can be distinguished (Jung, 1946), but according to Prof. Bout of Le Puy (private information) there is no break in the sequence and the series seems to range over a short interval of time. In the three localities recorded above there is no trace of the cold climatic phase that marks the beginning of the Pleistocene.

The fauna of the immediately following cold phase is perhaps represented in the solifluction deposits of Vialette, in the highlands of southern France (see Bout & Cailleux, 1951). In my opinion this cold phase might correspond to the Günz glaciation and marks the beginning of the Pleistocene.

In the Upper Valdarno basin the first lacustrine phase is overlain uncomformably by a second lacustrine series (Merla, 1949), and to this only is the term Villafranchian generally applied by Italian geologists. Its lower portion, not exposed, has been explored by borings and has yielded a flora that seems to indicate a cold climate. In the exposed section probably two horizons can be distinguished palaeontologically, a lower horizon with *Mastodon arvernensis* and an upper horizon with *Elephas meridionalis*, although these two species may have lived together for a short period (Merla, 1949; Azzaroli, 1950).

The fauna of Olivola (Azzaroli, 1950) is contemporary with the lower section with *Mastodon*, that of Tegelen (Hooijer, 1947) with the upper section with *Elephas*. The latter, according to Woldstedt (1950, "Tegelenschichten") is of an immediately pre-Elster age, that is, it belongs to the Günz-Mindel interglacial.

The end of this period is probably represented by the faunas of some solifluction deposits of southern France (Bout & Cailleux, 1951; Bout & Azzaroli, 1953, and private information from Prof. Bout). Sénèze (Schaub, 1944) is perhaps the most celebrated of these deposits. Other localities are Sainzelles and the Creux de Peyrolles. Perhaps also the loessic deposit of St. Vallier (Viret, 1948) should be placed here. These faunas are decidedly younger than that of Vialette and may be correlated with the Mindel glaciation, that marks therefore the close of the Villafranchian.

In England the Pleistocene starts with the Red Crag (Lagaaij, 1952). The mammalian fauna of this horizon is represented by poor fragments, among the most interesting of which are *Mastodon arvernensis*, *Elephas* cf. *planifrons*, two species of *Megaceros*, and *Euctenoceros falconeri*. This horizon presumably corresponds to the unexposed section of the Villafranchian Valdarno series. The equivalent of the highest section of the same series, and of the clays of Tegelen, is represented in England by the Weybourn Crag of Norfolk (see also later).

It is no easy task to state the fate of all the species of the main Villafranchian fauna, as the relationships of many of them with the representatives of later faunas are not yet clear. *Sus strozzii, Euctenoceros ctenoides, E. dicranios, E. tetraceros, Dama nestii, " Cervus " philisi* and its allies, *Meganthereon meganthereon, Brachyprosopus vireti, Gazellospira torticornis, Nemorhoedus meneghinii, Procamptoceras brivatense, Nyctereutes megamastoides* and *Acinonyx pardinensis* have left no descendants in the later faunas. This is possibly true also for *Leptobos*; a doubtful *Leptobos*, however, has been recorded from Süssenborn (Merla, 1949 : 49). The destiny of the horses is less clear, as this group still needs revision (Stehlin, 1932–33 : 51 ff.). The same difficulty arises for many carnivores; *Epimachairodus* survived for some time, and the larger felids, canids and bears might perhaps have evolved into more modern species (Stehlin, 1932–33, Schaub, 1949). The voles, represented in the Villafranchian by the primitive *Microtus*, underwent a gradual evolution which sets them among the most useful leading fossils for the Lower and Middle Pleistocene (Hinton, 1926; Schreuder, 1936, 1943, 1950; Heller, 1933, 1939; Van der Vlerk & Florschütz, 1950). A similar evolution was carried out by the elephants, although things are here less simple than they were thought at first (Trevisan, 1953). Also *Libralces* seems to have evolved further (see section " Palaeontology "). *Dicerorhinus etruscus* has been recorded also from post-Villafranchian deposits, but is represented there by more advanced forms (Soergel, 1923). *Hippopotamus* is found in the Villafranchian and in later times; its history may be one of successive immigrations and retreats (Stehlin, 1932–33). *Macacus* and *Castor* also survived, but their remains do not indicate whether they underwent any great change. *Trogontherium boisvilletti* seems to have survived unchanged in France and the British Isles (Schreuder, 1951).

The following phase is marked by the immigration of new faunal elements from Eastern Europe or from Asia: primitive red deer (*Cervus acoronatus, C. benindei* and other poorly known forms), the roe, wild boars of the group of *Sus scrofa* (probably represented by a distinct variety; Soergel, 1923), *Gulo gulo, Bos primigenius, Bison priscus.*

The voles evolved from *Mimomys* into primitive *Arvicola* (*A. greeni, bactonensis, mosbachensis*). A primitive *Microtus* has also been recorded from Mosbach. *Libralces* seems to have evolved from *L. gallicus* into *L. reynoldsi*, and the elephants from *Elephas meridionalis* into various races of *E. antiquus* and *E. trogontherii.* The group of *Megaceros verticornis* flourished in this period and possibly evolved *in situ.* Probably also the rhinoceroses and many carnivores are descendants of Villafranchian ancestors.

The best representatives of this period are the main faunas of Mosbach and Süssenborn, and the fauna of Mauer, in Germany; the fauna of Tiraspol in Bessarabia (Pavlow, 1906); the Needian of the Netherlands (Van der Vlerk & Florschütz, 1950), and some fossiliferous sands in the Upper Valdarno, around the village of Bucine (horizon 3 in Merla, 1949 : 51). These sands overlie comformably the Villafranchian, with the interposition of a series of barren gravels. In England the equivalent of these deposits is represented by the estuarine section of the Forest Bed series.

The dating adopted here is in contradiction with some current views and needs explanation.

Soergel (1928) assumed an early Mindel, if not even a pre-Mindel age for the fauna of Mauer. This was deduced from the occurrence of five horizons of weathered loess above the fossiliferous sands—a rather unsafe way of arguing, inasmuch as the age of the deposit depends on the number of glacial phases we admit. Soergel assumed two stages in the Würm (Weichsel) glaciation, two in the Riss (Saale) and two in the Mindel (Elster); but recently Woldstedt (1950) described four phases in the Weichsel glaciation and three in the Saale. These are sufficient to explain the occurrence of even more than five horizons of weathered loess above deposits of the great interglacial, and any evidence for attributing Mauer to the Mindel glaciation falls short. On the other hand, positive evidence for attributing these faunas to the Mindel-Riss interglacial is afforded by the Needian of the Netherlands, which corresponds to the *Paludina*-beds representing the great interglacial in Northern Germany (Woldstedt, 1950).

In 1932 Solomon placed the Forest Bed series of Norfolk in the first interglacial and assumed that the overlying glacial drift included representatives of the Mindel (North Sea Drift), Riss (Great Eastern) and Würm (Little Eastern) glaciations. But some of the difficulties met with in identifying Solomon's North Sea Drift with the Mindel glaciation and with the Norwich Brickearth of southern Norfolk were stressed a year before by Boswell (1931), and were given again by Boswell and by Hazzledine Warren in the discussion following the presentation of Solomon's paper. Solomon's evidence of a Mindel-Riss horizon within the glacial drift, assumed to be afforded by his " mid-glacial sands," is not conclusive, as these sands are barren and form no continuous horizon. In the dating adopted here the second (Mindel) glaciation falls between the Weybourn Crag and the Estuarine Bed. Its deposits, represented in southern Norfolk by Boswell's Norwich Brickearth, may have been cut out in north Norfolk by the erosion at the base of the Estuarine Bed.

The distribution of the *Bovidae* seems to have been influenced by geographic or climatic factors. The bison is recorded at Mauer, Mosbach and Süssenborn, whereas the aurochs makes its appearance in Central Europe during the Riss glaciation (probably in a mild interstadial). On the other hand this species is not uncommon in the sands near Bucine in the Upper Valdarno, with *Cervus* cf. *elaphus* and *Elephas antiquus*, which, from their position, cannot be much younger than the Villafranchian, whereas the bison is recorded in Italy only from the Upper Pleistocene. Possibly *Bos* immigrated into Italy along the southern slope of the Alps, whereas for some unknown reason it avoided Central Europe, and *Bison* did the reverse. In the gravels of Tiraspol, with a faunal assemblage characteristic of the stage of Mauer and the upper sands of the Upper Valdarno, *Bos* and *Bison* occur together. Unfortunately *Bos* is represented only by limb bones (Pavlow, 1906).

A later phase is marked by the appearance of more advanced species of *Arvicola*, evolved *in situ*, and by a widespread occurrence of *Microtus*, probably immigrants; but there does not seem to be any well-marked break in the fauna. *Dama clactoniana*, recorded only from the British Isles, belongs to this period.

The incoming Riss (Saale) glaciation seems to have extinguished *Dama clac-*

*toniana* and many species of the group of *Megaceros verticornis*. *Elephas primigenius*, or a related form, occurs for the first time at the beginning of this phase, but became common only after a mild oscillation, well marked at Steinheim a.d. Murr. In this mild interstadial the giant deer are represented here by *Megaceros antecedens* (Berckhemer, 1941) and the red deer by *Cervus elaphus angulatus* (Beninde, 1937). In the following cold phase the red deer is represented by a modern form and *Coelodonta antiquitatis* makes its very first appearance as an immigrant. The date of the immigration of the reindeer is less clear. Soergel (1943) recorded it from Steinheim, Mosbach and Süssenborn, but I have been unable to check the dating of these specimens. They are all said to belong to the tundra group (*R. arcticus*). Also *Ovibos moschatus* has been recorded from Süssenborn (Soergel, 1941).

At the end of the Riss glaciation (late Drenthian) the voles are represented by modern forms. A good guide fossil for the post-Rissian is *Megaceros giganteus*.

### *The Distribution of the Deer of the Norfolk Coast and their value for Stratigraphy*

As stated above, the deer of the Forest Bed series *sensu lato* include representatives of different faunas. Two faunas are quite distinct, whereas the existence of a third fauna is vaguely indicated by the deer, and is demonstrated conclusively only by other mammals.

The earliest fauna belongs to the upper section of the Villafranchian. It can be correlated with the horizon of Tegelen, Sénèze, and the ferruginous sands of the Upper Valdarno, and is represented by *Libralces gallicus*, *Euctenoceros tetraceros*, *E. ctenoides*, cervid cf. *Dama nestii nestii*. This fauna occurs in the Weybourn Crag.

The second fauna belongs to the second interglacial and corresponds stratigraphically to the classic faunas of Mosbach (main fauna), Mauer, Süssenborn (main fauna) and Tiraspol. Its representatives are *Libralces reynoldsi*, *Cervus* cf. *elaphus*, *Megaceros verticornis*, *Capreolus capreolus*. This fauna occurs in the Estuarine Section of the Forest Bed.

The third fauna, corresponding to a later horizon of the same interglacial, is probably indicated by *Dama clactoniana*, associated with *Cervus* cf. *elaphus*, *Megaceros verticornis*, *Capreolus capreolus*. This fauna occurs, partly at least, in the Upper Freshwater Bed. Possibly there is no true break between the two younger faunas.

The distribution of these species is not uniform throughout the outcrop of the Forest Bed series *s.l.* The Villafranchian species are restricted to the western section of the outcrop; they are very common at East Runton, where they are not accompanied by later faunal elements, and at Sidestrand, associated with younger species; rare at West Runton, Overstrand and Mundesley. Some doubtful and much-rolled specimens have been found also at Pakefield, at the eastern extreme of the outcrop. The second fauna occurs in all the localities, with the exception of East Runton, where only a few much-rolled specimens have been found.

The poorly represented fallow deer, supposed to represent the third fauna, is recorded from Bacton, Trimingham, and from the Upper Freshwater Bed at West Runton. Other representatives of this fauna have been recorded by Hinton from the Upper Freshwater Bed at Bacton and West Runton (see later), but this fauna might be more widespread.

Many localities have therefore yielded a mixed fauna, whereas a few of them have yielded more uniform faunas. Of particular interest are East Runton, with a pure Villafranchian fauna, and the Upper Freshwater Bed of West Runton, which, also on geological grounds, can be assumed to include only representatives of the "third" fauna. This distribution may give a clue to an approximate dating of the remaining species, not known or doubtful in other districts.

*Libralces minor* is recorded only at East Runton and Sidestrand; it belongs therefore to the Villafranchian fauna.

*Libralces latifrons* from Happisburgh (doubtful at Mundesley, Cromer and Walcot) may belong either to the second or the third fauna.

*Euctenoceros sedgwicki*, from Bacton and Mundesley, probably belongs to the second fauna. The presence of the large fallow deer and the absence of *Libralces reynoldsi* at Bacton would rather suggest a later age, but the absence of *E. sedgwicki* in the very fossiliferous Upper Freshwater Bed of West Runton is, perhaps, more significant. This species is possibly present also at St. Prest.

*Megaceros dawkinsi* and *M. savini* are probably of the same age. They do not occur in the Upper Freshwater Bed of West Runton, nor at East Runton. *M. dawkinsi* has been recorded also from the Weybourn Beds at Weybourn by Savin, but the name of the horizon was possibly taken from the locality and it would be unsafe to rely on this statement. This species, or a related form, seems to have been widespread in continental Europe.

The dating of "*Cervus*" *obscurus* is more doubtful, but this species probably belongs to the second interglacial.

### *The Evidence Afforded by Other Mammals on the Age of the Forest Bed Series*

The list of the other mammals from the Forest Bed *s.l.* also gives the impression of a mixed fauna. We need only mention the occurrence of four species of elephants, a fact not recorded from any other locality in Europe.

The elephants still need revision, and it would be unsafe to assume the alleged *Elephas primigenius* as evidence of the existence of an early Rissian horizon in the Forest Bed series. But the evidence afforded by the voles (Hinton, 1926; 1926*a*) is more conclusive, and demonstrates the existence of an horizon equivalent to the Swanscombe gravels.

The "shelly crag" at East Runton yielded Villafranchian representatives (*Mimomys pliocaenicus*, *M. intermedius*, *M. savini*), whereas the Upper Freshwater Bed at West Runton yielded a mixed fauna: *Mimomys intermedius*, *M. savini*, *M. maiori*, *Evotomys* sp., *Pitimys arvaloides*, *P. gregaloides*, *Microtus arvalinus*, *M. nivalinus*, *M. nivaloides*, *M. ratticeppoides*. This is certainly not evidence of the presence of different horizons in the Upper Freshwater Bed, as the older species may easily have been washed in. The age of the deposit is indicated by the younger species and corresponds to the early Drenthian (Van der Vlerk & Florschütz, 1950). The same species of *Microtus* have been found also in the middle gravels of Swanscombe (Schreuder, 1950). A correlation between the Upper Freshwater Bed and Swanscombe has been made also by Hinton (1926*a*, 336–337). Shortly later Mochi (1929 : 179–181) proposed a correlation of the Norfolk sequence with the earliest glaciations that agrees substantially with that stressed in these pages and differs only in minor details.

## SUMMARY

GEOLOGY AND CHRONOLOGY. The mammal bearing horizons of the Norfolk coast include three horizons separated by unconformities: the Weybourn Crag, the Estuarine Bed or Forest Bed *s. str.* and the Upper Freshwater Bed. The whole series rests on a levelled surface of chalk and is capped by glacial drift. The so-called Forest Bed Fauna is actually made of three successive faunas. The oldest one, from the Weybourn Crag, is of upper Villafranchian age and is assumed to correspond to the first (Günz-Mindel) interglacial. Its representatives are: *Euctenoceros ctenoides, E. tetraceros, Libralces gallicus, L. minor,* and a small species perhaps identical with *Dama nestii nestii.* The second fauna, from the Estuarine Bed, is contemporary with the main faunas of Mosbach, Süssenborn, Mauer, Tiraspol, and the horizon of Neede, and is assumed to correspond to the second interglacial. Its representatives are: *Megaceros verticornis, M. dawkinsi, M. savini, Libralces reynoldsi, Cervus* cf. *elaphus, Capreolus capreolus,* and possibly *Libralces latifrons, Euctenoceros sedgwicki* and "*Cervus*" *obscurus.* The third fauna, from the Upper Freshwater Bed and possibly also from the highest section of the Estuarine Bed, is contemporary with the gravels at Swanscombe and with the early Drenthian and corresponds to a later period of the same interglacial. It is represented by a species possibly identical with *Dama clactoniana,* together with *Megaceros verticornis, Cervus* cf. *elaphus* and *Capreolus capreolus.* Conclusive evidence of its age is afforded by small rodents.

PALAEONTOLOGY. *Alcinae* and *Capreolinae* were differentiated from the *Cervinae* before the Upper Miocene. The Upper Miocene *Cervinae* belong to two quite distinct lineages. In eastern Europe they are represented by *Damacerus bessarabiae* (= *Cervocerus novorossiae*) and *D. variabilis* (= *Procervus variabilis*), and may perhaps have evolved into the Villafranchian *Cervus ramosus.* In China they are represented by three-tined deer (incorrectly identified with *Cervocerus novorossiae* by former authors), from which probably most of the Pleistocene and living *Cervinae* took origin. The phyletic development of antlers is also discussed.

The deer of the Weybourn Crag and Forest Bed *s.l.* belong to the genera *Libralces, Capreolus, Cervus, Euctenoceros, Megaceros* and possibly *Dama*; there is in addition a species of *Cervinae* of uncertain affinities.

*Libralces* is a close ally of *Cervalces. L. gallicus* is smaller than living elks, but *L. reynoldsi,* which is probably its descendant, is the largest deer hitherto known. *L. latifrons* and *L. minor* are poorly represented.

The roe also is poorly represented.

The earliest representatives of *Cervus s. str.* were more primitive than the living European red deer; some of them were similar to living red deer of Central Asia. The red deer of the Forest Bed also seem to be primitive, but their remains are not satisfactory.

*Euctenoceros* is distinguished by peculiar features of the antlers. Its most primitive representative is *E. falconeri* from the Red Crag. *E. sedgwicki* is possibly its descendant. *E. ctenoides* (= *E. teguliensis*) and *E. tetraceros* do not differ from the types from other Villafranchian localities.

*Megaceros* can be divided into two groups, based on characters of the skull and antlers: the group of *M. giganteus* and the group of *M. verticornis*. *M. savini* is a primitive species of the group of *M. giganteus* and its antlers are not palmated. *M. verticornis*, the commonest species of deer in the Forest Bed, has large and widely palmated antlers. *M. dawkinsi* belongs to the same group; it is smaller and has secondarily reduced antlers, and a hypsodont dentition.

"*Cervus*" *obscurus* is a large species of quite unusual features and of unknown affinities. Its remains are scanty.

Two much smaller species may possibly be identified with *Dama nestii nestii* and with *Dama clactoniana*.

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BY
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# A CONIFEROUS PETRIFIED FOREST IN PATAGONIA

*By* MARY G. CALDER

## SYNOPSIS

The present paper contains the results of a detailed investigation of a large collection of silicified coniferous remains from the remarkable petrified forest of Cerro Cuadrado, Patagonia.

Conclusive evidence of only two species (*Araucaria mirabilis* and *Pararaucaria patagonica*), based on seed cones, has been found. *Araucaria mirabilis* belongs to section *Bunya* of the genus *Araucaria*, and the affinities of *Pararaucaria patagonica* are probably with the Taxodiaceae: both species are extinct. The associated wood, branches, twigs and seedlings probably belonged to one or other of the species described. The age of the forest is uncertain, and is at present placed somewhere between Middle Jurassic and Wealden.

## INTRODUCTION

THE existence of petrified coniferous plant remains in regions west of the mouth of the Rio Deseado in the province of Santa Cruz, Patagonia, appears to have been first noted scientifically by Dr. A. Windhausen of the Argentine Geological Survey. In 1919 he discovered silicified cones which were kept as curios in stores and farms in the country south-west of the Gulf of San Jorge; and in 1923 he found abundant petrified material of conifers *in situ* in the region of the Cerro Alto (or Cerro Chato), near the Estancia Belgrano, in a locality about S. lat. 47° 50′ by W. long. 68° 40′ (Windhausen, 1924 : 203, footnote). His collection of silicified wood and cones was passed on to Professor Gothan of Berlin, who gave a short description of them (Gothan, 1925). Dr. Carlos Spegazzini had also (1924) briefly described silicified twigs and cones, the latter similar to those found by Windhausen, which he had received from various donors: these specimens were from the region of the Cerro Madre y Higa, a small volcanic peak about 30 miles north-east of Windhausen's locality (Spegazzini, 1924). Meantime, during 1923–24, a palaeontological expedition from the Field Museum of Natural History, Chicago, had been collecting fossil mammals in Eastern Patagonia, and Dr. Elmer S. Riggs and others made an additional expedition to the region of the Cerro Madre y Higa, and its neighbouring peak about 10 miles to the west, the Cerro Cuadrado, where they found " a considerable number of fossil trees, some with stumps standing, others lying prone with broken branches and cones scattered about them, revealing a forest of fossil Araucaria or Brazilian Pines preserved on the site where it had grown " (Riggs, 1926 : 544; Wieland, 1935 : 6).

These discoveries made it clear that in the region of the volcanic peaks of the Cerro Cuadrado, Cerro Madre y Higa, and Cerro Alto, in a district about 10° south of the modern forest of *Araucaria araucana* (Molina) ( = *A. imbricata* Pav.) in Chile and Argentina, and about 26° south of the forests of *Araucaria angustifolia* (Bertol.) ( = *A. brasiliana* Rich.) in Southern Brazil, there existed the petrified remains of an extensive araucarian forest. The large Field Museum collection made by Riggs and his co-workers was later reviewed by Wieland (1929, 1935); his vividly-presented memoir, however, was without detailed anatomical studies of critical features. A fuller account of one of the cones in the Field Museum, with special reference to the embryo, was given by Darrow (1936). After this, little further botanical investigation of the petrified forest was undertaken, subsequent accounts by Darrah (1939 : 222), Florin (1940 : 36), Arnold (1947 : 313) and Andrews (1947 : 175) being recapitulations of earlier studies, though Florin's later work (1944 : 513) gave a partly revised interpretation of the structure of one type of cone. A non-botanical account of the petrified forest is presented in the memoir by Wehrfeld (1935) of a journey through Santa Cruz. The geology of the regions between the Rio Deseado and the Rio Chico where the forest is situated has also been recently reviewed by Feruglio (1949 : 118; 1951 : 35), with special reference to fossil floras of plant compressions found at other localities in this area.

Important new collections of the conifers of the petrified forest have, however, been made by Dr. Franz Mansfeld in the region of the Cerro Alto whilst searching for fossil vertebrates, and in 1936 the British Museum (Natural History) acquired an extensive collection of some 600 specimens from him, some by presentation and some by purchase. Similar material is also widely distributed in other museum and departmental collections: a demonstration of some of it was given by W. T. Gordon at the Geological Society of London on behalf of Dr. Mansfeld (Gordon, 1936). The collection in the Geology Department of the British Museum is a representative one; in it are included silicified woods, branches and twigs of various sizes, seedlings, and cones, in varying states of preservation and offering remarkable evidence on the nature of the conifers of the petrified forest. The present account is based mainly on this material, though reference has also been made to specimens in other collections: Professor Gothan has described some of this more recently-collected material from specimens in Berlin and elsewhere (Gothan, 1950) and reference is made to this description when the seedlings are discussed. A more detailed study of these South American petrified conifers, and in particular, of the cones, appears to be desirable, especially in view of recent developments in studies of the taxonomy and morphology of the living Araucariaceae (White, 1947; Wilde & Eames, 1948, 1952; Buchholz, 1949) and of the fossil Araucariaceae (Kendall, 1948, 1949; Cookson & Duigan, 1951). In addition, the remarkable extension and organization of knowledge of the taxonomy, morphology and distribution of fossil conifers in general provided by the work of Florin (1931, 1940, 1938–45) give a more critical basis for comparative interpretation than was previously available.

## LOCALITY AND AGE

The site of the petrified forest is in the neighbourhood of the small volcanic peaks of the Cerro Alto (Chato), Cerro Cuadrado, and Cerro Madre y Higa, to the south of the Rio Deseado in the region between lat. 47°–48° S., long. 68°–69° W. (cf. Gothan, 1925, pl. 10; Wieland, 1935 : 6, text-fig. 1). More recent accounts of the area where the silicified plant remains are found have, however, shown that the extent of the forest is considerably wider than suggested in earlier reports. Feruglio's survey (1949 : 128, map opposite p. 134 ; 1951 : 69, 74) indicates a number of additional localities where cones and branches occur, some 25–30 miles to the north-west of the Cerro Alto : these are, Estancia Los Toldos, Canadon de las Cuevas, and west of Cerro Botellon. According to Feruglio's maps, there are at least two localities in the region south of the Rio Deseado called " Cerro Cuadrado " : one lies between the Cerro Alto and the Cerro Madre y Higa in the area originally indicated for the petrified forest, and another some 70 miles to the south-west near to the Estancia La Guitarra. From the latter locality Feruglio has described a quite separate mixed flora consisting of compressions including some araucarian remains (1951 : 62–65, 69), to which reference will later be made. Feruglio's review of the region of the Cerro Alto where the petrified araucarian remains are found (1949 : 128) does not include the vicinity of the Cerro Cuadrado, after which Wieland named the forest, as one of the fossiliferous localities ; the Cerro Alto appears to be the central locality of the forest, and also to be one which has produced very valuable and representative collections, though no doubt much remains to be discovered in other areas..

It is clear, from the various descriptions, that the forest was overwhelmed in an outburst of volcanic activity, the plant remains being embedded in a rhyolitic volcanic ash. Some are found lying weathered out on the surface, showing varying degrees of erosion of surface features, and some of the tree stumps are still standing as noted, for example, by Riggs (1926 : 544), and illustrated by Frenguelli (1941, pl. 25, fig. 1) ; Frenguelli's photograph shows widely scattered trunks, and not a close-set forest formation. Numerous seedling stems, to which reference will later be made, also tend to confirm the impression that the forest was preserved *in situ*, and was overwhelmed whilst regeneration was in progress.

The exact geological age of the forest is still doubtful. Dr. Mansfeld suggested that the rocks from which his specimens were collected were not older than Cretaceous, and that they might even be of Tertiary age ; these estimates appear to have been based on the comparatively modern appearance of the plant structures, rather than on geological data (Gordon, 1936). The horizon has been placed, in other accounts of the petrified forest, as widely apart as mid-Triassic (Windhausen, 1924 : 203 ; 1931 : 201 ; Gothan, 1925 : 197 ; Wieland, 1929 : 60 ; 1935 : 8), Cretaceous (Florin, 1940 : 36 ; 1944 : 513) and Eocene (Frenguelli, 1933, cf. Darrow, 1936 : 328, and Fossa-Mancini, 1941 : 68). Dr. A. F. Leanza, of the University Museum of La Plata, Argentina, very kindly informed me (*in litt.*, 19th June, 1948) that geologically it could then only be indicated that the forest belonged to some stage in the Mesozoic. Windhausen dated the forest as Triassic in the belief that the volcanic ashes which enclose the plant remains form part of an eruptive which, in the geological correlations then in vogue, was comparable in age with the eruptive cycle which in the province of Mendoza originated the porphyritic series found beneath sediments containing a *Thinnfeldia* flora ; eruptive cycles are, however, now known also to have occurred in Patagonia at later stages in the Mesozoic. Feruglio has reviewed again, in some recent publications (1949 : 118 ; 1951 : 35) to which Mr. W. N. Edwards very kindly drew my attention, the problem of the geologic age of the forest. He describes a series of floras of plant remains in the form of compressions from a number of outcrops of the complex of volcanic sediments (the " porphyritic series of Bahia Laura ") in the region between the Rio Deseado and the Rio Chico; and compares them in detail with floras of mid-Jurassic to Wealden age, with special reference to species of *Hausmannia*, *Cladophlebis*, *Nilssonia*, and *Ptilophyllum*. He concludes that the age of the volcanic series is in large part between mid-Jurassic and Wealden; and that the age of the petrified forest around the Cerro Alto, which occurs in the same complex (although its exact stratigraphic position in relation to the other floras has not been determined), must lie somewhere within the same range (1949 : 131; 1951 : 74). Feruglio also points out that a major unconformity separates this volcanic series from the Upper Cretaceous; and also that the original determination of a species of *Estheria* from this series in this area as being of Rhaetic age is not now generally accepted. These latter points further support his delimitation of the age on the basis of the floras.

## PRESERVATION AND TECHNIQUE

The plant remains are silicified: the replacement of the organic matter has been fairly complete, and the specimens have not been effectively sectioned by any adaptation of the cellulose peel technique. Thin petrological slices have accordingly been used (prepared by Mr. J. Fowler of Sheffield) where details of the tissues are required. However, in some specimens or parts of specimens the silicification has gone so far that little detail can be distinguished: in others the wall structure is well defined, and such details as the nature of pitting in the xylem, and the structure of the embryos in some of the cones, may be observed. The cut and polished faces of the cones may be used quite effectively for general morphology in many cases; Wieland relied very largely on this means of examination in his description of the types (Wieland, 1935), which was accordingly lacking in histological details that have proved to be of considerable importance to the interpretation of the general morphology and taxonomy. Cut and polished specimens form very pretty curios, as the preservation is in rather light silica enhanced by a variety of chalcedonic shades of colour. Darrow (1936 : 330) has already commented on the tendency for the various tissues of the seeds to be preserved in distinctive shades of quartz.

## (1) FOLIATED AND DEFOLIATED TWIGS AND BRANCHES

### ***Araucarites sanctaecrucis*** n. sp.

(Pl. 1, figs. 4–6, 8–13)

1924. *Araucarites ?* Spegazzini, p. 133, text-fig. 4 (8).
1935. *Proaraucaria mirabilis* (Speg.): Wieland, p. 27, pl. 13, fig. 1.

DIAGNOSIS. Woody branches of araucarian habit, radially symmetrical, 5–25 mm. in diameter, occasionally with lateral axillary branches in one row or two opposite rows. Evergreen: leaves or leaf-scars arranged in a spiral with angle of divergence 3/8 or 5/13, the latter on the thicker branches. Leaves imbricate and more or less appressed. Leaf rhomboidal, 8–14 mm. in length, 4–8 mm. in width at its broadest region, tapering distally to a subacute, somewhat incurved apex, the margins converging at the apex at an angle of 60°–80°. Abaxial surface sometimes showing parallel longitudinal ridges and grooves. Free part of leaf flat, about half the length of the entire leaf, and seated on a flat leaf-base cushion, from which on older branches it has been shed. Leaf-base cushions on older branches 20–30 mm. wide, 5–10 mm. high, with marked longitudinal fissures. Venation of leaves and structure of epidermis not known. Secondary xylem, seldom preserved, with uniseriate and contiguous bordered pits on radial walls of tracheids.

LECTOTYPE. The specimen figured by Spegazzini, 1924, fig. 4 (8).

HYPOTYPE. V. 30941. Geol. Dept., B.M. (N.H.). The specimen illustrated in this paper (Pl. 1, figs. 8, 10, 11).

LOCALITY AND HORIZON. Cerro Alto, Santa Cruz, Patagonia: Between mid-Jurassic and Wealden.

DESCRIPTION.—Many of the detached branches show one side of the specimen much weathered, with surface features nearly obliterated, and the other with excellent preservation of external morphology (Pl. 1, figs. 8, 10, 11). No doubt the better preserved surface was that which lay downwards on the forest floor, whilst the upper surface was subject to processes of weathering as the surrounding rhyolitic volcanic ash was worn away; some specimens of leafy branches are still embedded in the ash (Pl. 1, fig. 1 at *L*), but most are detached. Pl. 1, figs. 4, 9, 10, 11 and 13 illustrate the habit of branches of varying age. Pl. 1, fig. 11 shows an unbranched stem probably four years old, while figs. 4 and 9 represent thinner branches, probably penultimate branches of the shoot, and show axillary branches similar to that (? 1 year old) in fig. 13, which tend to be arranged in two opposite rows or one row on the parent branch. This condition is found in the penultimate branch systems of many conifers where dorsiventrality in respect of the ultimate branching is common. The defoliated branch of lower order (Pl. 1, fig. 6) may represent the broken apical region of a terminal main branch, with 3 laterals in an apparent whorl.

In the foliated shoots the leaves are arranged in spiral phyllotaxy with angle of divergence 3/8 or 5/13, the latter on the thicker branches: Church (1904 : 99) has noted such spirals of a higher order on the thicker leafy branches in the Recent *Araucaria excelsa*. Pl. 1, fig. 10, *t*, shows the free lamina of the leaf, and at *b* the leaf-base cushion, from the stem shown in Pl. 1, fig. 11. This specimen demonstrates that these plants were evergreen: in transverse section as seen in the cut surface at the upper end (Pl. 1, fig. 8), it shows poorly preserved secondary xylem with 3–4 rather ill-defined growth rings, probably annual. It also shows in some patches of the poorly preserved secondary wood that the radial pitting of the tracheids is uniseriate and contiguous as illustrated in Pl. 1, figs. 3, 7. The transversely cut face (Pl. 1, fig. 8, *t*) also shows the free part of the leaf in sectional view, demonstrating its flat, unkeeled nature. No veins are preserved in the leaf, so that the broad-based leaf habit cannot be definitely associated with parallel venation: nor can the longitudinal striation which is seen on the abaxial surface of the leaf in some specimens (e.g., Pl. 1, fig. 5) be definitely associated with any anatomical feature such as ribs of sclerenchyma. The furrows in such cases may represent the position of lines of stomata, but it has not been possible to demonstrate these structurally, either from sections or cuticles. The older defoliated branch seen in Pl. 1, fig. 12, probably about 5 years old, shows tangentially-extended leaf-base cushions without any clearly-defined scar of attachment of the free lamina of the leaf : it is doubtful whether the longitudinal fissuring in such specimens is entirely a natural condition following on the stretching of the bark with increase in secondary thickening, but it is a common feature in some living araucarians (cf. *A. araucana*, Seward & Ford, 1906, pl. 23, fig. D).

In none of the specimens figured or described in previous accounts of the forest is there any indication of foliated branches : those referred to by Spegazzini (1924) and by Wieland (1935) as *Araucarites ?* and *Proaraucaria mirabilis* respectively are similar to that figured in Pl. 1, fig. 12 of the present account, which has been interpreted as an older branch where the free lamina of the leaf has been shed. After comparison of the variation in morphology of branches of different age in, for example, the living *Araucaria araucana* (cf. Seward & Ford, 1906, pl. 23, A–G), there would seem to be no reason for regarding these thicker defoliated branches as a separate species in the absence of any further criteria of difference : the structure of the secondary xylem is too infrequently and inadequately preserved to be used as such. Various references to similar branches (Darrow, 1936 : 333, 337—where they are identified with *Proaraucaria mirabilis*,—and Arnold, 1947 : 314) have compared them with the living South American species of *Araucaria*, *A. araucana* and *A. angustifolia*, which comprise the section *Columbea* Endlicher, emend. Wilde & Eames. However, from the locality Meseta de Baquero, about 70 miles to the south-west of the Cerro Alto petrified forest, Feruglio has recently described compressions of leafy branches as a new species of *Araucaria*, *A. grandifolia* (Feruglio, 1951 : 62, pl. 3, fig. 5), and he suggests that these might belong to the cone species *Proaraucaria mirabilis*, from the petrified forest, whose vegetative organs, he says, are not known (1949 : 137). He adduces no botanical reasons for this suggestion of relationship, and it is presumably based on geographical propinquity. Comparison of the habit of *A. grandifolia* with that of the leafy branches here described certainly does not suggest specific identity between the sterile branches from the two localities, for *A. grandifolia* has much larger leaves, long, rather narrow, pointed and lanceolate, and of spreading habit. There are no cuticular studies of this species, and on the evidence of the external morphology alone one might even hesitate to assign the branches to the genus *Araucaria*.

Although the general habit of the foliated shoots from the petrified forest suggests comparison with an araucarian type, they cannot be identified on the basis of their external morphology with any living species of *Araucaria*. It is true that the flat and rather broad laminae of the leaves more closely resemble those of the living species of the sections *Columbea*, *Bunya* and *Intermedia* of the genus *Araucaria* than they do those of section *Eutacta* (cf. Wilde & Eames, 1952 ; White, 1947) ; but the combination of characters represented by their relatively small size and flat, somewhat scale-like habit, broad base and rhomboidal form and appressed and imbricate arrangement cannot be matched in any known living species. Indeed, in the absence of information on leaf venation and epidermal characters there is no sound justification for their inclusion in the genus *Araucaria* ; and the only other existing genus in which they might conveniently be placed is *Araucarites*. *Araucarites* has been used to define fossil cones or shoots of araucarian habit, for various reasons not identifiable with the genus *Araucaria* itself (Seward, 1919 : 256),—though Seward pointed out (pp. 265–6) that the use of this generic name for sterile shoots is not in accordance with sound principles. More recent detailed studies of " araucarian " sterile shoots (*Brachyphyllum*, *Pagiophyllum* : Kendall, 1948, 1948*a*, 1949) have demonstrated that fossil genera which may be distinguished from *Araucaria* in cuticular structure may have this habit ; though in the case of *Brachyphyllum mammillare* (Kendall, 1949) it is almost certainly related to cone structure resembling that of *Araucaria*. Where, as in the present material, it is not possible to make cuticular investigations, or any definite assignation to fertile material, it is most convenient meantime to retain the artificial genus *Araucarites* to include these branches, which are certainly of araucarian habit. As will be noted in a later section of this paper, the sterile branches are associated with seed cones of two highly distinctive types, one of araucarian and the other probably of taxodiaceous affinity : and in the case of the latter the foliation of the cone pedicel may be superficially compared with that of the separate leafy shoots, which have not been found in connection with cones. The foliated and defoliated shoots may even include more than one species amongst them, though at present these cannot be differentiated. The name *Araucarites sanctaecrucis* is instituted for these sterile shoots, after the province in which the petrified forest occurs.

### (2) WOODS

(Pl. 1, figs. 2, 3, 7.)

These are represented by a large number of unbranched woody stems varying from about 8 cm. to 0·5 cm. in diameter, a few being still partially embedded in the rhyolitic ash (Pl. 1, fig. 1, w). Most of these specimens have a complete thick cylinder of secondary xylem, but no distinctive external features : Pl. 1, fig. 2 shows a stem where part of an outer zone, probably representing remains of bark, may be distinguished (*c*). The preservation of the tissues, so far as examined, is so poor that extensive cutting does not appear to be warranted : but it has been possible to make a few observations on the wood structure. In the stem shown in transverse section in Pl. 1, fig. 2, there is a narrow pith (*p*), and endarch primary xylem groups surrounded by a wide zone of secondary xylem (*x*) with several somewhat indeterminate growth rings, probably 12 in number. In radial longitudinal section the pitting of the radial walls of the tracheids of the secondary xlyem can be observed only in a few isolated patches where the organic matter of the walls has probably not been entirely replaced during silicification : this is illustrated in Pl. 1, figs. 3, 7. The bordered pits are uniseriate and contiguous with slight flattening of outline where they adjoin ; but the structure of the medullary rays has nowhere been observed. In another larger specimen (8·5 cm. in diameter : V 30976), probably from a branch 16 years old as judged by the ill-defined growth rings, similar uniseriate pitting has been observed, but again without preservation of medullary ray structure. This wood type so far as it can be defined is not identical with that reported by Gothan

(1925 : 198, pl. 1, figs. 1, 2) and Wieland (1935 : 16) in other specimens from the same locality. Gothan's wood, named by him *Dadoxylon* (*Araucarioxylon*) sp., showed radial tracheid walls with uniseriate bordered pits, sometimes distantly separate and rounded, sometimes contiguous, but with the indication of the cross-field pitting too indefinite for satisfactory use.

Uniseriate contiguous pitting of the tracheids such as is illustrated here was a type widely represented in the Mesozoic (cf. Seward, 1919 : 165 ; Kräusel, 1949) by a variety of " genera " of fossil woods e.g., *Mesembrioxylon* and *Brachyoxylon*. It has from time to time been interpreted as one transitional phyletically between the " pinacean " and " araucarian " types as these were formerly more or less rigidly defined (e.g., Hollick & Jeffrey, 1909 : 75) : Wieland regarded the Cerro Cuadrado woods as representing such a transitional type (1935 : 16). However, it has more recently been demonstrated that this type of xylem pitting cannot be regarded as necessarily indicative of transitional or ancestral Araucariaceae, since it is found within the range of variability in xylem structure in individual plants in modern genera of different families of the Coniferales (e.g., *Pinus* : Bailey, 1933 ; *Sequoia* : Bailey & Faull, 1934 ; Araucariaceae : Pool, 1929). According to Pool (1929 : 599) it is more common in the stem wood of Araucariaceae than is usually recognized.

Without more details of the wood structure, therefore, and in particular of the medullary rays on which keys for wood identification have laid stress (Gothan, 1905 ; Kräusel, 1919, 1945 ; Phillips, 1941), it is not possible to make any effective comparison or identification of these woods. As will presently be shown, they are associated with two types of cone, one araucarian and the other probably most nearly related to the Taxodiaceae ; and the wood just described might have belonged to either–it corresponds closely with that described for the cone axis of the latter type. Similar wood structure has also been found, very poorly preserved, in the sterile foliated branches of araucarian habit already described. But it cannot be identified more specifically than as coniferalean wood.

It may be noted in conclusion that Wehrfeld (1935) referred to abundant remains of araucarian petrified wood in the forest, but he adduced no evidence of structural detail. His illustrations are of uncut woody trunks and branches, some showing " annual " rings (e.g., p. 120, pl. f), and some of the trunks were very large, one incomplete specimen being reported as 100 metres in length (p. 125). If this were confirmed, it would seem that some of the trees of the Cerro Cuadrado petrified forest were perhaps the tallest that ever lived, and certainly the tallest that have been found in a petrified state. One would like to have precise measurements, not only of length, but of diameter at intervals throughout the length. As Fossa-Mancini has pointed out (1941 : 75), the theoretical maximum height of about 300 feet propounded by Galileo for a tree (cf. Thompson, 1942 : 28) was no doubt considerably exceeded by such a tree as that mentioned by Wehrfeld : and other reports (Feruglio, 1949 : 129) have also recorded very wide trunk bases in the forest. Leanza is quoted by Feruglio (1949 : 129, footnote) as reporting the base of a fallen trunk of circumference 10·3 metres (i.e., diameter approx. 3·26 metres). These accounts of gigantism in the trees of the petrified forest refer to the trunks as araucarian ;

as there is no account of wood structure to corroborate this, the identification has no doubt been made on the evidence of associated cones. The wood structure of branches so far examined structurally, as has been pointed out, is indefinitive in character for purposes of identification ; and as will later be shown, while one of the cone types found in the forest is araucarian, the other is probably most nearly related to the Taxodiaceae, in which family at the present day occur the most striking examples of gigantism in trees, comparable with those of the petrified forest. It is perhaps more likely that these giant petrified trunks belong to this family than to the Araucariaceae, but more information on the details of their wood anatomy is needed.

Wehrfeld also reported finding, more rarely, wood of palms. His description of these mentions woods showing yellowish spots which he interpreted as the remains of the principal vascular bundles ; but no structural evidence was given to support this interpretation, nor has it so far been possible to obtain evidence of the presence of monocotyledons from any other woods examined. The " yellowish spots " which he described may represent variation of the mineral differentiation in the stems rather than the position of vascular bundles ; for the petrifactions in the forest tend to show differentiation of colours in the quartz.

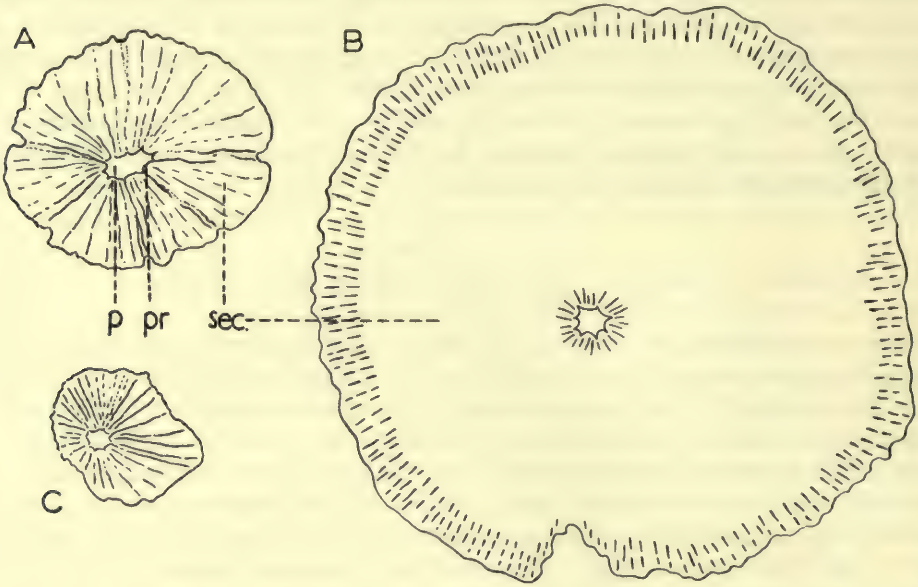
### (3) SEEDLINGS

(Pl. 2, figs. 14–25 ; Text-fig. 1, A–C.)

There are numerous (about a couple of hundred) petrified structures, many of them looking like small corms or carrots, which vary in shape from ellipsoidal to turbinate (Pl. 2, figs. 14, 15, 17,), with intermediate forms such as that shown in Pl. 2, fig. 16. Most of these specimens are detached : but Pl. 2, fig. 14 shows one (*s*) lying prone and partially embedded in the matrix. The turbinate forms vary in size from 4 cm. in height and 5 cm. in widest diameter to 1·5 cm. in height and 2·2 cm. in diameter ; the ellipsoidal or clavate forms are more uniform in size, averaging 4·5 cm. in height and 1·5 cm. in widest diameter. None of these structures shows any continuation at either end of the axis into a leafy shoot or a well-defined root : Pl. 2, figs. 18 and 19 show one specimen with a prolongation of the broader end of the axis which bears no evidence of insertion of lateral organs.

From external examination of the specimens and from examination of cut and polished surfaces it may be seen that most are partially or completely decorticated (Pl. 2, figs, 15, 17), and that a few have what appears to be a fairly thick periderm (Pl. 2, figs. 18–20, 22, *pd.*). The core of such specimens is composed of a thick zone of poorly preserved tissue resembling secondary wood (Pl. 2, figs. 19, 20, 22, *x*) and a narrow region in the centre probably comprising pith and primary xylem. The decorticated specimens show on their external surfaces longitudinal fissures and markings (Pl. 2, figs. 15–17), some of which might indicate the position of primary medullary rays in the xylem ; however, as such markings may also be found on corticated specimens (Pl. 2, fig. 18), they may be due, at least in part, to cracking during decay and preservation.

Some thin sections have been prepared from the more promising of these specimens with a view to studying the arrangement and detailed structure of the tissues for comparison with the gross morphology. The preservation is unfortunately very poor in most of the specimens cut: but Pl. 2, figs. 23–25 shows the centres of transverse sections taken at the top (broader) end, middle, and base (narrower end) of a specimen similar to that shown in Pl. 2, fig. 15, where preservation was better than in most. The outlines of the whole sections are shown in Text-fig. 1, A–C (corresponding with Pl. 2, figs. 23–25), where it can be seen that there is a medullated stele with the pith region (*p*) widening from the base upwards, whilst it also changes from rounded to ovate in shape in transverse section. Pl. 2, fig. 21 shows this pith in median longitudinal section of the broader end of the specimen; the innermost elements of the xylem ring are narrower than those forming the bulk of the xylem, and the pith is notable for its more or less isodiametric, thick-walled cells. The bulk of this specimen is composed of poorly preserved tissue resembling secondary xylem traversed by medullary rays, in which structure of pits cannot be distinguished. The primary xylem groups which abut on the pith increase in number from below upwards, and the condition appears to be endarch, with stem structure throughout, and with no evidence of traces passing out to lateral appendages. Other sections from specimens similar to those in Pl. 2, figs. 16, 17 show the same general arrangement of the tissues (cf. Pl. 2, fig. 22); the structure of the tissue resembling secondary xylem can only be distinguished in a few better-preserved patches in some of the



TEXT-FIG. 1. Seedling (cf. *Araucaria mirabilis*). Transverse sections through a seedling at top, middle and base of swelling (cf. Pl. 2, fig. 15), showing pith (*p*) in centre surrounded by primary xylem groups (*pr*) and secondary xylem (*sec.*). (cf. Pl. 2, figs. 23–25). V. 30951. × 5.

longitudinal sections, where coniferalean pitting, of the type illustrated in Pl. 1, figs. 3 and 7, may be distinguished on the radial walls.

These curious bodies must therefore be interpreted as swollen intercalary organs, having stem structure but without any evidence of lateral appendages, and with marked development of a tissue resembling secondary xylem. Their identification is a matter of some difficulty ; but the structures are so numerous, and the intercalary swelling is so striking in all of them, that they must have some regular significance in the vegetation of the forest. Wehrfeld figured a number of such structures (1935 : 129), and referred to them as " a scientific novelty—a series of fossil araucarias," without, however, substantiating in any way the reference to the Araucariaceae. Gothan, too, in a recent brief study (1950), has described such structures as those in Pl. 2, fig. 17—the turbinate or fig-shaped forms—and believes the most likely interpretation to be that they are of the nature of insect galls, terminal on branches, where hypertrophy of the wood of the branch has been caused with the larva living in the centre, and with the gall eventually dropping off the end of the branch. He also believed they might be araucarian, but had found no evidence of any such galls in living Araucariaceae. It has not, however, been possible to find any evidence that the structures are other than intercalary, or that the turbinate forms are different in kind from the ellipsoidal forms ; and in some of the specimens sectioned there is a definite pith including thick-walled cells and with no sign of any larval intrusion. There remains, however, the possibility that these might be fungal stem galls of an intercalary nature ; such intercalary stem swellings are known in some cases to be caused by fungi, as in the case of *Peridermium* galls on *Pinus* stems ; but no records of such galls on araucarian stems have been found, though Connold (1909 : 132, text-fig. 159) has described long, irregular tumours on the roots of *Araucaria imbricata* which do not resemble the present structures at all. In the case of either terminal or intercalary stem galls, however, one would expect to find some evidence of lateral appendages, and there is none. On the other hand the size, shape and internal structure of these bodies all tend to emphasize their similarity to broken first-year seedlings of the genus *Araucaria* in the sections *Bunya* and *Columbea*, where tuberous development in varying degree is found in the hypocotyl, which is of stem structure with early incidence of secondary thickening (Dürr, 1865: 103; Hemsley, 1901; Seward & Ford, 1906 : 333 ; Shaw 1909 ; Hill & de Fraine, 1909 : 212 ; Hickel, 1911 : 160).

Wieland has figured certain branch-like structures (1935 : 27, pl. 13, fig. 2) as bases of second-year seedling stems of *Proaraucaria*, with broken root bases : but if these are indeed older seedlings, they are not markedly tuberous, and there is no evidence of any relationship with the smaller structures here described. The tuberous habit in seedlings in general is sporadic : it appears to be rare amongst gymnosperms, occurring in the Cycadales in *Encephalartos*, and in the Coniferales in the two sections of the genus *Araucaria* just mentioned. The proximity of these numerous tuberous bodies to fertile cones belonging to the section *Bunya* of the genus *Araucaria*, which will be described in the next section, also tends to corroborate their interpretation as araucarian seedlings : and the fact that the embryos in the seeds of these cones are dicotyledonous might suggest that the markedly ovate form of the pith at the upper end of the seedlings is related to a stelar adjustment below the level of the insertion of the vascular supply of two cotyledons on opposite sides of the hypocotyl axis.

So far as has been ascertained, this is the only record of petrified seedlings. Kendall (1949, text-fig. 1, J.) has drawn attention to a curious specimen, found as a compression, from the Mid-Jurassic Estuarine Series of Yorkshire which she has interpreted as a seedling stage of *Araucarites phillipsi* Carruthers, but no other such records are known to the writer.

Mr. W. N. Edwards informs me that there is a specimen in the Sedgwick Museum, Cambridge, from the Lower Greensand of Upware, Cambridgeshire, which was figured by Keeping (1883: 150, pl. 8, fig. 7) as " a small fruit (?) ferruginized," but which superficially at least is very similar to some of the smaller araucarian seedlings from Patagonia.

### (4) CONES

The cones, which represent the best preserved part of the collection, are of especial interest, since petrifactions of reproductive organs of fossil conifers are seldom found, though petrified coniferous woods are abundant. Two distinct types of seed cone are represented, but no male cones or pollen-producing organs have been found. These two types of cone have already been partially described by Spegazzini (1924), Gothan (1925), and Wieland (1935); but detailed studies of the structure, which affect the interpretation of the morphology and consequent assessment of the relationships of the cones, have not been made, with the exception of Darrow's investigation (1936) of the structure of the embryo of *Araucaria mirabilis*.

### ***Araucaria mirabilis*** (Spegazzini)

(Pls. 3, 4, 5; Text-figs. 2–4)

1924. *Araucarites mirabilis* Spegazzini, p. 126, text-figs. 1–3, 4 (1–7).
1925. *Araucaria windhauseni* Gothan, p. 200, pls. 2–7, pl. 8, fig. 1.
1929. *Proaraucaria mirabilis* (Speg.) Wieland, p. 60.
1929. *Proaraucaria elongata* Wieland, p. 60.
1931. *Araucaria mirabilis* (Speg.) Windhausen, p. 201.
1935. *Proaraucaria mirabilis* (Speg.): Wieland, p. 19, pl. 1; pl. 7, figs. 2, 3; pl. x; pl. xi, figs. 1, 2, 4; text-fig. 4.
1935. *Proaraucaria mirabilis* var. *elongata* Wieland, p. 26, pl. 8, fig. 1; pl. 9, fig. 2; pl. 12, fig. 4.
1935. *Proaraucaria patagonica* Wieland, p. 26, pl. 6, figs. B, D, E, F.
1935. *Proaraucaria mirabilis* var. *minima* Wieland, p. 26, pl. 6, fig. A; pl. 12, fig. 3.
1936. *Proaraucaria mirabilis* (Speg.): Darrow, p. 328, text-figs. 1–13.
1936. *Araucarites mirabilis* Speg.: Gordon, p. 14.
1939. *Proaraucaria mirabilis* (Speg.): Darrah, p. 222, text-figs. 133, 134.
1940. *Araucaria mirabilis* (Speg.): Florin, p. 36.
1944. *Araucaria mirabilis* (Speg.): Florin, p. 513.
1947. *Proaraucaria mirabilis* (Speg.): Arnold, p. 313, text-fig. 156.
1947. *Proaraucaria mirabilis* (Speg.): Andrews, p. 177, text-fig. 121.
1948. *Proaraucaria mirabilis* (Speg.): Wilde & Eames, p. 312.
1949. *Proaraucaria mirabilis* (Speg.): Feruglio, p. 129.
1951. *Proaraucaria mirabilis* (Speg.): Feruglio, p. 35.

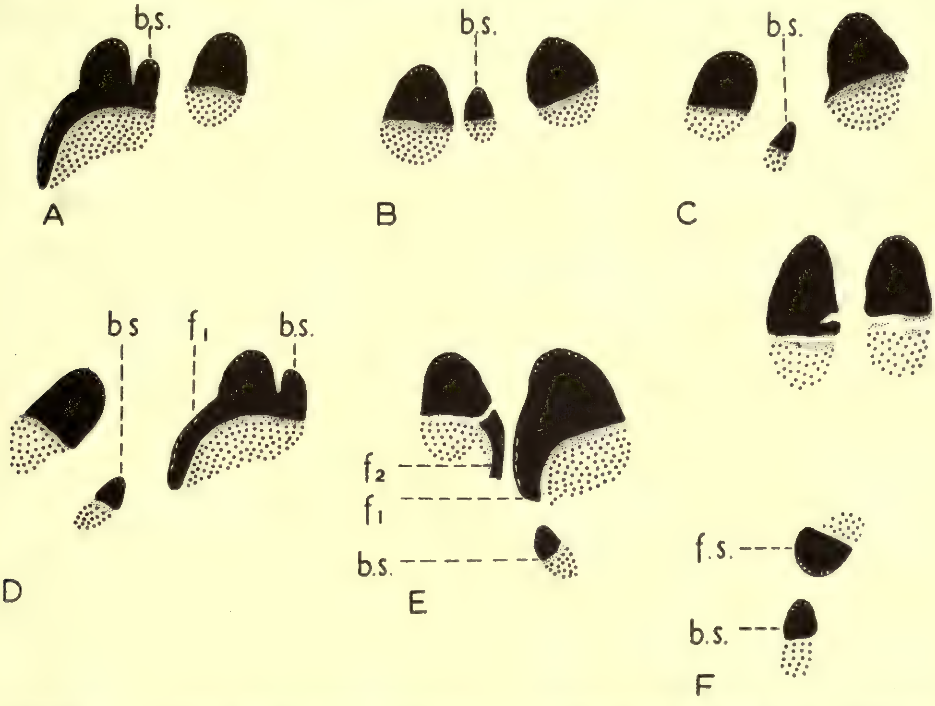
EMENDED DIAGNOSIS. Seed cones varying in shape from spherical to somewhat ellipsoid, and in size from about 8 to 4 cm. in height and 8 to 4 cm. in diameter. Cone-scales numerous, arranged in a close spiral, one-seeded, with thick woody wing and deciduous laminar tip, which on dropping reveals the large woody ligule on top of the rhomboidal apophysis of the bract; the fertile scale is fused with the bract for about two-thirds of its length, so that the depth of the ligular sulcus is about one-third of the length of the fertile scale. Cone-scales of mature seed cones (delaminated) 13–16 mm. long and 10 mm. wide including the wing, tapering somewhat towards the base. Ligule 4 mm. wide, 1·2 mm. high, about 5 mm. long. Seed 8 mm. long and 3 mm. wide and deep, inverted, albuminous, apparently embedded in the fertile scale tissue; testa with a thick stony layer. Embryo large, dicotyledonous, with numerous spirally twisted suspensors at base. Evidence on mode of seed dispersal lacking.

Axis of cone wide, with a wide pith including branched sclereids, surrounded by a narrow ring of separate vascular bundles each with a wide outer sheath of fibrous extra-phloem tissue. Vascular supply of cone-scale double, the bract trace single and arising separately from the base of the leaf-gap in the axis stele, the fertile scale supply of two strands, arising from either side of leaf gap, which fuse with inversion: both bract and fertile scale supply fork in base of cone-scale to give a lower and an upper (inverted) series respectively, the lower series passing out to the apophysis and laminar tip of the bract accompanied by a series of resin canals, the upper series terminating in the large strongly vascularized ligule.

DESCRIPTION.—The species is represented by a large number of specimens in the collection; most of these are isolated specimens, but a few are still partially embedded in the matrix (Pl. 3, fig. 26). Some of the cones must have been mature, as they contain fully formed embryos in the seeds, while others have no embryos, though the cones may be as large as those which do. The cones vary in size from 8 cm. in length and diameter to 4·4 cm. and 4 cm. in length and diameter respectively, and in shape from nearly spherical to ovoid or ellipsoid. There is no evidence to suggest that the smaller cones are necessarily immature, for one about 5 cm. in length and diameter (V. 30975) has fully formed embryos in the seeds. Some specimens appear more markedly elongate, with an ellipsoidal section, than others (e.g., Pl. 4, figs. 38, 42): such cones were interpreted by Wieland (1935 : 26) as a distinct variety, *Proaraucaria mirabilis* var. *elongata*, but structurally it has not been possible to differentiate these types, and there is evidence from the cone figured here that the condition has been exaggerated by considerable crushing prior to petrifaction, as may be seen in the compressed and broken outer parts of the scales in Pl. 4, figs. 40, 42, while the proximal part of the scales has withstood the compression, being reinforced, perhaps, by the woody tissues of the testa. The cones have been petrified before the shedding of the seeds in most cases; no separate petrified seeds nor cone-scales have been found, but there are a few specimens, such as those figured by Wieland (1935, pl. 6, E) and interpreted by him as another species, *Proaraucaria patagonica*, which no doubt represent the naked axes of the cones after the cone-scales have been shed (e.g., V. 30969). They correspond in size with the measurements of the cone axes themselves; one has been sectioned, and shows a wide pith with sclereids, and peripheral vascular bundles. The surface features correspond closely with those found in cones of living araucarians after shedding of the cone-scales (cf. Seward & Ford, 1906 : 361), with a reticulum of low ridges outlining rhomboidal areas no doubt representing the areas of attachment of the scale bases to the cone axis. The absence of any separate cone-scales, which Gothan (1950 : 153) has emphasized as a feature suggesting that these cones did not shed their scales at maturity, and as one which might separate them generically from those of other species of *Araucaria*, may well be explained in terms of the season in which the forest was overwhelmed. The seeds in the cone-scales in the final year of growth had not been shed, and the previous year's had germinated and are probably represented in the forest by the very numerous petrified seedlings to which reference has already been made.

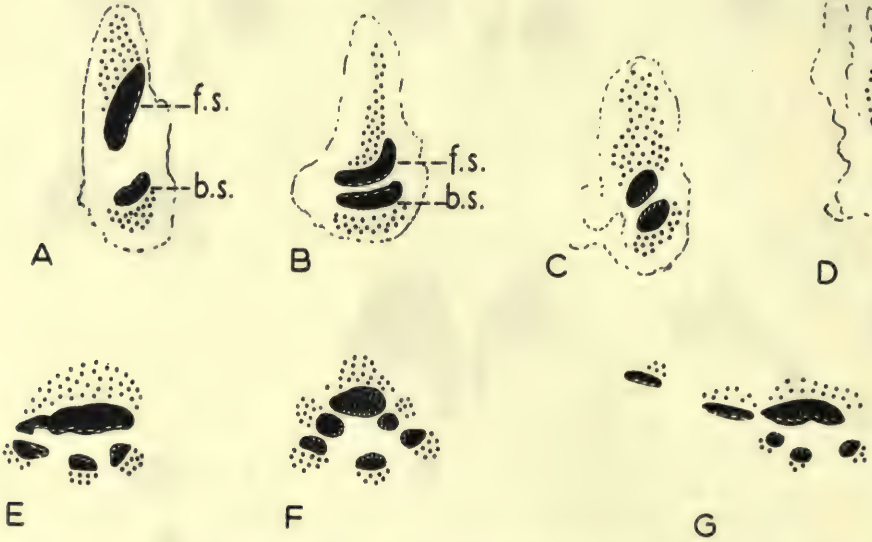
Various views of external features of cones are shown in Pl. 3, figs. 26–31, Pl. 4, figs. 38, 39, and Pl. 5, fig. 46. Inserted on the cone axes are a large number of close-set ligulate cone-scales, each of which bears a single large inverted seed sunken in its tissue on the upper surface. The distal, abaxial faces of the cone-scales are seen arranged in a close spiral forming some 55 orthostichies (so far as has been examined). The surface morphology of the cone-scales varies, probably according to the age and condition of the cone and also to some extent to the degree of weathering of the surface, as shown in Pl. 3, figs. 28, 29, 31, 34, Pl. 4, figs. 38, 39, and Pl. 5, fig. 46. Pl. 4, figs. 38, 39, 42 show a cone where in surface view the cone-scales have laminar, longitudinally striated tips (*t*). In earlier descriptions of the cones, Gothan (1925, pl. 2) and Spegazzini (1924, text-figs. 1*b*, 4 (6)) have illustrated some with a similar triangular lamina on the cone-scales, and Wieland mentions this feature (1935 : 175, pl. 10, fig. 2). Most of the cones, however, show surface morphology of cone-scales as illustrated in Pl. 3, figs. 28, 29, and Pl. 5, fig. 46, with prominent apophysis of bract (*a*) with marked lateral wings (*w*), and a large ligule (*l*). Consideration of sections of the specimen in Pl. 4, figs. 38, 42, leaves little doubt that this latter condition is the result of the dropping of a laminar tip, though erosion of surface features may occasionally account for it. Pl. 4, figs. 40, 42, show this laminar tip *t*, covering the ligule *l*, in radial longitudinal section ; and Text-fig. 4, A–I, and Pl. 4, fig. 43, Pl. 5, fig. 54, from a tangential longitudinal series, demonstrate the same relationship between the laminar tip and the ligule. There is, too, some structural evidence of an absciss zone at the base of the laminar tip, e.g., at A in Pl. 4, fig. 40. The lateral wings of the cone-scales are also seen to be present in the series of tangential sections, though they tend to be obscured in surface view (Pl. 4, fig. 39) as compared with the cones with delaminated scales. In any respect other than the presence or absence of a laminar tip it is difficult to separate the two cone types : in both, seeds with fully formed dicotyledonous embryos of the same type have been found. The much smaller cone illustrated in Pl. 3, figs. 31–34, shows similar longitudinally striated laminae clothing the exterior of the cone ; in section (Pl. 3, figs. 32, 33) no ovules can be distinguished, and it may be either a young cone or one with abortive or unpollinated ovules. The comparatively large ligule can again be distinguished behind the distal lamina of the cone-scale (Pl. 3, fig. 33, *l*). There seems little doubt that the three cone types just described represent different stages in the development of the same cone species; in many of the living Araucariaceae there is a laminar tip or spine on the cone-scale which often drops off when the cone is ripe (cf. Pilger, 1926 : 255).

The ligulate cone-scales are modified in form towards the base of the cone, where they are sterile. Pl. 3, fig. 30 shows the transversely cut tip of a cone pedicel (*pl*), around which are a number of such sterile cone-scales of simplified form, which pass over gradually into the fully formed fertile cone-scales above. This is a character of araucarian cones which has been emphasized by Seward & Ford (1906 : 354, text-fig. 22A) as contrasting with the condition in the Pinaceae where the cone-scales are much more sharply differentiated in form from the foliage leaves, and succeed them more abruptly. In none of the fossil cones examined is there critical evidence of the foliation of the pedicel, or of attachment to any of the leafy branches which are found amongst the remains of the forest.



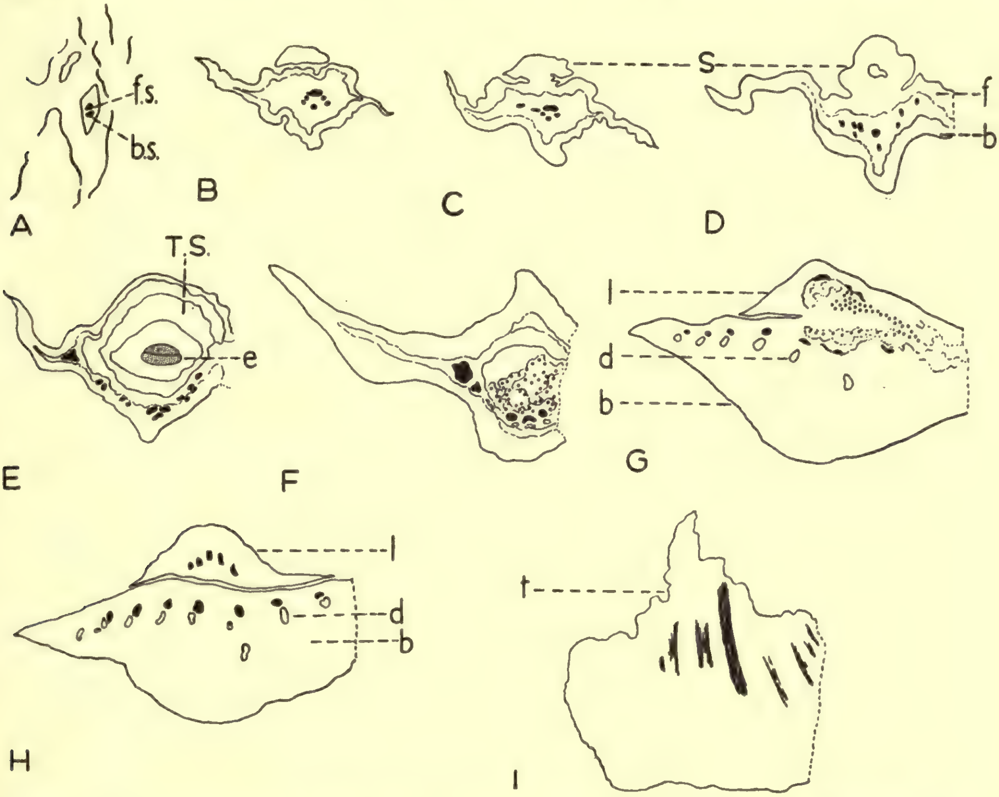
TEXT-FIG. 2. *Araucaria mirabilis* (Spegazzini). Transverse sections through vascular bundles of cone axis stele, showing from base upwards a series in the detachment of the bract supply (*b.s.*) and fertile scale supply (*f*1, *f*2) of cone scales. The two traces of the fertile scale supply fuse with inversion to give a single bundle (*f.s.*). The pith lies to upper side, cortex to lower side, of the vascular bundles, where xylem is shown black, with protoxylem white, phloem finely stippled, and extra-phloem tissue coarsely stippled. V. 30958. × 27·5.

The axes of the cones are thick (Pl. 3, fig. 27), with a wide pith and narrow ring of separate vascular bundles, seen at *p* and *v* respectively on the transversely fractured surface and in Text-fig. 2 in transverse section. The pith contains branched sclereids; the tissues of the vascular bundles are ill-preserved, but in patches of better preserved tracheids the xylem pitting varies from uniseriate to biseriate and alternating, with the pits separate, and each bundle is endarch, with a narrow zone of phloem, outside which is a deep arc of extra-phloem tissue (? pericycle) as seen in Text-fig. 2, *e.p.* This extra-phloem tissue is much better preserved than is the phloem, and consists of large, thick-walled, sometimes branching cells resembling the sclereids of the pith rather than a typical fibrous tissue. Comparison of this type of cone axis with that of other conifers reveals the striking similarity with that of living araucarian cones. Thomson (1913 : 4) has drawn particular attention to the exceedingly large size of the pith in the cone axis of the Araucariaceae, especially in the seed cones, where it may reach 1 in. in diameter. The sclereids of the pith and the extra-phloem or fibrous pericyclic tissue are, too, characters associated with the axis anatomy of the living Araucariaceae (cf. Seward & Ford, 1906 : 337).



Text-fig. 3. *Araucaria mirabilis* (Spegazzini) (cf. cone in Pl. 4). Tangential longitudinal sections of cone-scales from base outwards, showing splitting of the two bundles *b.s.*, *f.s.*, in base (cf. Text-fig. 2), to give the vascular supply of bract and fertile scale respectively. Xylem shown black, with protoxylem white, extra-phloem tissue coarsely stippled. V. 30957. × 27·5.

A study of the detachment of the cone-scale vascular supply from the axis stele has been made in transverse sections of the cone axis; Text-fig. 2, A–F, illustrates successive stages, from below upwards, in the detachment of the traces, as seen in different sectors of the wide cylindrical stele. This has proved more satisfactory than the use of a series of sections, as 1·5–2 mm. may be lost between successive sections in preparing a series, while the spiral succession of the numerous scales is so close-set that from one section a close series of stages can be obtained. The bract supply, *b.s.*, comes off as a single trace from the base of the leaf-gap, and free from the fertile scale supply, *f.s.*, which is derived from the fusion of two strands, *f*1, *f*2, detached separately from either side of the leaf-gap above the bract supply. These two strands rotate through 180° while fusing, so that the resultant fertile scale fusion bundle is inverted (Text-fig. 2, D–F). In the base of the cone-scale there are, therefore, two bundles, the upper one inverted. Text-fig. 3 shows their subsequent behaviour in tangential sections of the cone illustrated in Pl. 4, fig. 38, taken in series from the inside of the cone outwards: Text-fig. 4, from the same series, shows the relationship of the bundles to the cone-scale morphology throughout the scale and into the laminar tip. Each of these two bundles in the scale base branches, the bract bundle first (Text-fig. 3, D–E), and this lower series, though incompletely preserved in the region below the seed (Text-fig. 4, E, F), appears to supply the apophysis and the laminar tip of the bract (Text-fig. 4, G, H, I; cf. Pl. 4, fig. 43; Pl. 5, fig.



Text-fig. 4. *Araucaria mirabilis* (Spegazzini) (cf. cone in Pl. 4, and Text-fig. 3). Tangential longitudinal sections of cone-scales from base outwards, to show vascularization of bract (*b*), its laminar tip (*t*), and fertile scale (*f*) with ligule (*l*). Xylem shown black, sclerotic tissue coarsely stippled. *S* = seed, *T.S.* = stony layer of testa, *e* = embryo, *d* = resin ducts, *f.s.* = vascular supply of fertile scale, *b.s.* = vascular supply of bract. V. 30957. × 5.

54). In the outermost region of the cone-scale (Text-fig. 4, G, H, and Pl. 5, fig. 54) structures resembling resin canals (*d*) lie below the bundles. Pl. 4, figs. 43, 45 show obliquely cut bundles (*v.b.b.*) supplying the laminar tip of the bract ; these bundles are accompanied on either side by a strand of cells with dark contents (*d*), which may represent the upward extension of the resin canals into the laminar tip. It has not been possible to demonstrate whether, as in *Araucaria bidwilli*, there is a distinct system of bundles ending blindly in the apophysis, with the laminar supply branching off farther back.

The upper inverted fertile scale bundle branches farther out in the scale base (Text-fig. 3, E–G), and forms a strong inverted upper series, probably supplying the base of the single inverted seed (Text-fig. 4, F) as well as the large ligule (Text-fig. 4, G, H, and Pl. 5, fig. 54). Pl. 4, fig. 44 demonstrates a vascular strand in the ligule. Pl. 5, fig. 53, taken from a delaminated cone, also demonstrates vascularization of the large ligule (*l*), along with the distinct series of the bract (*b*).

There are two notable features here for comparison with the living species of *Araucaria* : the separate origin of the bract and fertile scale supplies, and the strong vascularization of the ligule. Only in the section *Bunya* Wilde & Eames amongst the living araucarians are these two conditions found (Eames, 1913 : 24 ; Aase, 1915 : 297 ; Wilde & Eames, 1948 : 322 ; 1952 : 44). This is probably the first time that it has been possible, in a fossil araucarian cone, to demonstrate these characters, which are of critical importance in considering the taxonomy and interrelationships of living araucarians.

Text-fig. 4 and Pl. 5, fig. 54, also serve to demonstrate the lateral winging of the cone-scale ; this " winging," already noted in the external morphology of the cones, extends from near its base out to the apophysis, as seen in Text-fig. 4, B–H. A similar condition is found in the delaminated cone shown in Pl. 5, figs. 46, 50, 53. The wing is about as wide as the body of the seed, and is relatively thick ; it is supplied by vascular bundles of the lower (bract) series (Text-fig. 4, G, H, and Pl. 5, fig. 54). The tissues of the wing have evidently been woody, as may be seen in the cone in Pl. 5, fig. 50, where a core of thick-walled pitted cells is found, possibly of the nature of a transfusion tissue, and in Pl. 5, figs. 53, 54 where there is a deep hypodermal zone of thick-walled cells. Cone-scales as thick and woody and as widely winged as these must have been are found amongst living araucarians only in the section *Bunya* (Wilde & Eames, 1952 : 44).

The morphology of the ligule, already noted in surface view of the cones, is seen in tangential longitudinal sections in Text-fig. 4, G, H, Pl. 5, figs. 53, 54, and in radial longitudinal section in Pl. 4, fig. 40, Pl. 5, fig. 52. Its vascular bundles have already been noted ; its ground tissue is similar to that of the wings, and no doubt it was also woody. The depth of the sulcus between the ligule and the bract may be exaggerated by artificial splitting between the two, extending apparently deep into the scale, the space occupied by clear quartz. The cone in which the split is most clearly and perhaps most naturally seen is illustrated in Pl. 3, figs. 35–37 : it will be noted that, where the scale is not quite medianly cut as at A in the radial longitudinal section of the cone in Pl. 3, figs. 35, 36, the split extends deeper than the level of the base of the seed, but where a more median cut of the seed is found, as at B, the split stops towards the base of the seed. This is also demonstrated in the tangential longitudinal series of another cone in Text-fig. 3, F–H, where in Text-fig. 3, G, just outside the base of the seed, the ligule has separated from the bract on the margin but not yet in the median plane. It will be seen from Pl. 3, figs. 35, 42 that the ligular sulcus is about one-third the depth of the fertile scale, the fertile scale being fused with the bract for about two-thirds of its length; and this is about the same proportion for the depth of the ligular sulcus as in the living *Araucaria bidwilli* in mature cones (cf. Wilde & Eames, 1948: 325; Pilger, 1926: 256, text-fig. 139, A). Wieland based his generic definition of these cones as *Proaraucaria* on the greater depth and size of the split separating ligule from bract, as well as on the larger size of the ligule, in comparison with the condition in living species of the genus *Araucaria* (Wieland, 1935: 19), and he regarded the fossil species as representing an intermediate stage in the evolution of the cone-scale, with less complete fusion of bract and fertile scale. His figures, however, nowhere make clear the natural depth of the split separating ligule from bract. From the present examination there is no evidence to show that the difference in degree of size of ligule and depth of sulcus separating it from the bract in the fossil and in living species is such as to warrant the erection of a new genus; the fossil is closely similar to *Araucaria bidwilli* in these respects.

The relationship of the seed to the upper surface of the scale is shown in Text-fig. 4, B–G, Pl. 4, figs. 40–42, and Pl. 5, figs 47, 50–52. The single large inverted seed (S) appears as if embedded in the scale tissue; this is probably best seen in the tangential sections in Pl. 5, figs. 47, 50, the conspicuous stony layer of the testa (T.S.) lying within an outer sheet of tissue (F) which is continuous with the surface tissue of the wing of the scale on either side of the seed. Within the stony layer the nucellus is imperfectly preserved, but in many seeds the embryo sac may be defined, enclosing the endosperm with an embryo embedded in it (Pl. 5, figs. 47, 50–52, *en* and E). The dicotyledonous embryo is seen entire in Pl. 4, fig. 41, where the polished radially cut surface of the cone is photographed; and embryos are seen cut in transverse section of the cone at E in Pl. 5, figs. 48, 51, and Text-fig. 4, E, in tangential longitudinal sections of the cone in Pl. 5, figs. 47, 49, 50, and in radial longitudinal sections in Pl. 4, figs. 40–42 and Pl. 5, fig. 52. Plate 4, fig. 41 and Pl. 5, figs 48 49 demonstrate the two cotyledons (*co*), and Pl. 4, figs. 41, 42, show the orientation of the embryo with the thick radicle pointing towards the micropylar end of the embryo sac, where there is a tangled mass of suspensors (*ss*) (Pl. 5, fig. 51). The embryo need not be described in detail as this has been done by Darrow (1936); but dicotyledonous embryos of similar type have been found in both the laminated and delaminated types of cone (cf. Pl. 4, fig. 42, Pl. 5, figs. 47–51), and the orientation of the plane in which the median lines of the two cotyledons lie varies from one more or less parallel to the surface of the fertile scale (Pl. 5, figs. 47, 49) to one at right angles to it (Text-fig. 4, E).

RELATIONSHIPS. From the fuller account of these araucarian cones which it has now been possible to give and with particular reference to the critical characters of mode of origin of the vascular supply of the cone-scale from the axial stele, size and nature of wing of cone-scale and size and nature of ligule, two major conclusions emerge which contrast with many of the previously expressed views on the relationships of this species. The first is that there are no grounds for its taxonomic separation into a new genus *Proaraucaria*, which was effected by Wieland (1935) because he believed the cleavage between ligule and bract to be deeper than in any living species of *Araucaria*. Gothan later (1950 : 153) suggested, without further description of the cones, that the fact that they did not appear to shed their cone-scales at maturity was a character of major importance in separating the genus *Proaraucaria* : this condition has been discussed in an earlier section, where it was concluded that there is no evidence that the cones did not shed their scales, but a certain amount to suggest that they did. The second major conclusion is that the nearest related living species of *Araucaria* is *A. bidwilli*, the only species so far included in the section *Bunya* recently erected by Wilde & Eames (1952) in their taxonomic revision of the genus *Araucaria*, and found to-day only in Eastern Australia in Queensland. Most of the previous references to these fossil araucarians have compared them with the two living South American species, *A. araucana* and *A. angustifolia* ; though Darrow compared the fossil cones with *A. bidwilli*, this was not substantiated by any critical study of the vascularization or of the ligule, but she effectively demonstrated the structure of the embryo, which is similar to that in *A. bidwilli*. It is true that in the fossil species there is no evidence for dehiscence of the individual cone-scales, for no separate seeds nor empty scales have been found ; and this character is one of those on which Wilde & Eames differentiated their new section *Bunya* (1952 ; 44). But in general structure of the cone-scale and ligule, and in particular of their vascularization, there is a striking similarity between the living *Bunya* and the fossil species : indeed, the larger size of the cones of *A. bidwilli*, which may reach 30 cm. in diameter, appears to be the chief difference between the species as represented by the cones. The use of the generic name *Araucarites* for these cones, though it has taxonomic priority, is best set aside (cf. also Florin, 1940 ; 1944) : for this name is reserved for cones or branches of araucarian habit which, however, are lacking in preservation of structural details which might give final evidence justifying inclusion in the genus *Araucaria* itself. The name *Araucaria mirabilis* (Speg.) is therefore used, and the species is assigned to the section *Bunya* Wilde & Eames, the only other species of this section being the living *Araucaria bidwilli*, which is found to-day only in Queensland.

The proximity of these cones to the seedling structures already described is certainly significant, though there is no evidence of organic relationship. Tuberous seedlings are known amongst living species of *Araucaria* only in the section *Bunya* and in the South American section *Columbea*. The rarity of such a seedling habit in gymnosperms has already been noted ; and so far as records have been examined it is not found in any of the Taxodiaceae, to which the only other fertile cones in this area where the seedlings are found probably belong.

Similarly, the proximity of the cones to the leafy branches of araucarian habit which have been described as *Araucarites sanctaecrucis* may be of significance, though evidence of attachment of cones to such branches is missing ; but as will presently be shown, the foliation of the pedicel in the *Pararaucaria patagonica* seed cones does not rule out the possibility that the branches, or some of them, may have been related to this quite distinct type of cone.

## ***Pararaucaria patagonica*** Wieland

(Pls. 6, 7 : Text-figs. 5–7)

1929. *Pararaucaria patagonica* Wieland, p. 60.
1929. *Pararaucaria elongata* Wieland, p. 60.
1935. *Pararaucaria patagonica* Wieland, p. 21, pls. 2–5.
1936. *Pararaucaria patagonica* Wieland : Gordon, p. 14.
1937. *Pararaucaria patagonica* Wieland : Darrah, p. 223.
1940. *Pararaucaria patagonica* Wieland : Florin, p. 36.
1944. *Pararaucaria patagonica* Wieland : Florin, p. 513, pl. 184, figs. 23–26.
1947. *Pararaucaria patagonica* Wieland : Arnold, p. 314.
1949. *Pararaucaria patagonica* Wieland : Feruglio, p. 129.
1951. *Pararaucaria patagonica* Wieland : Feruglio, p. 35.

EMENDED DIAGNOSIS. Seed cones, ovoid in shape, varying in length from 4·7 cm. to 2·3 cm. and in diameter from 2·4 cm. to 1·3 cm., borne on slender pedicels clothed with spirally arranged, imbricate, broadly lanceolate and somewhat acute leaves with longitudinal striation of the abaxial surface. Bracts bearing the axillary fertile scales usually about 38 in number in average-sized cones, large and conspicuous, probably woody, each subtending a thick fertile scale, and arranged in a closely imbricate spiral succession with angle of divergence 3/8. Bract 10 mm. long, 12 mm. wide, 1·5 mm. thick, free from fertile scale for greater part of length ; fertile scale 10 mm. long, 12 mm. wide, 2·5 mm. thick, showing longitudinal ridges on its protruding distal abaxial face, and bearing usually one large inverted seed, laterally inserted, flattened and winged, the seed separating from scale at maturity. Seed 6 mm. long, 6 mm. wide, 2 mm. thick, with wing 2 mm. wide tapering towards base and tip of seed ; testa with inner stony layer, and outer layers composing wing of a characteristic stellate sclerotic lacunar tissue. Embryo 4 mm. long, polycotyledonary ; seed probably exalbuminous.

Cone axis slender, with narrow pith and thick endarch cylinder of xylem. Succession of elements in primary xylem includes scalariform and reticulate tracheids, passing over into elements with biseriate bordered pits. Secondary xylem tracheids usually with uniseriate bordered pits, contiguous and flattened, the pit apertures rounded or ovate ; medullary rays with cross field pitting of cupressoid form. No resin ducts or cells present. Bract supply arises from axis stele as a single trace from base of leaf gap ; fertile scale supply arising as two traces, one from each side of leaf gap above bract trace, the two traces fusing to give inverted bundle, which is accompanied into the scale on the adaxial face by a large strand of sclerenchyma which forks into two. Bract and fertile scale supplies single in base, branching higher up, with an abundant transfusion tissue linking the bundles tangentially and persisting in tips of bract and scale when bundles die out. Seed supplied by a single lateral strand from supply of fertile scale.

DESCRIPTION. This species is represented by a large collection of mature seed cones ; no younger stages appear to be present, though it has been possible to section only a few of the specimens for more detailed examination. (One specimen, V. 30974, smaller than average with length 24 mm. and width 12 mm., probably represents an abortive or unfertilized cone, but preservation is not good enough for a convincing identification.) The species is redescribed here with special reference to a number of diagnostic characters which were not included in Wieland's original account (Wieland, 1935); it is the most interesting species in the collections from the Cerro Alto localities, and its relationships with other conifers have not so far been assessed by comparison of a sufficiently wide range of characters. It may be of interest to note here that Feruglio (1949 : 129) reports, in a review of the localities where the plants of the petrified forest are known to occur, that *Pararaucaria* has been found only in two of the localities with petrified cones, viz., the Cerro Alto, where it is associated with the cones of *Araucaria mirabilis*, and near the Estancia Los Toldos, where the latter species is missing.

The general habit of the cones is illustrated in Pl. 6, figs 55, 56, 63. They vary in length from 4·7 cm. to 2·3 cm., and in diameter from 2·4 cm. to 1·3 cm., the average size being about 4 cm. long and 2 cm. in diameter. There is no evidence that smaller cones represent younger stages; they probably represent attenuated cone forms, bearing fewer appendages. This range in size corresponds with that observed by Wieland in his specimens. A longer cone type was originally separated by him (1929 : 60) as *Pararaucaria elongata*, but later (1935 : 21, pl. 5, fig. 6) he included this type in *Pararaucaria patagonica*. A similar long cone is shown here in Pl. 7, figs. 74, 75; and no other distinctive characters have been noted in it. These long cones are often poorly preserved and much weathered, as in Pl. 7, fig. 74, but the bract and fertile scale show the same proportions as in smaller specimens. Cones of average size as well as these long cones have been found to contain fully developed embryos in the seeds (Pl. 6, fig. 58; Pl. 7, fig. 75), a condition refuting Wieland's suggestion that the latter represent the mature seed cones, while the former are immature. Such a range in size is a feature quite common in the cones of, for example, living species of *Pinus*.

The cones are somewhat ovoid in shape; many show marked unilateral weathering of the surface features and some a varying degree of compression. The specimen in Pl. 6, fig. 63, approaches most nearly to the condition of the surface features in the living plants. A number of large and conspicuous bracts (*b*), about thirty-eight in an average-sized cone, are arranged in a close-set spiral around the axis, with successive bracts overlapping and with an angle of divergence of 3/8 as in other cones observed. In the axil of each bract is the fertile scale (*f*), showing slight longitudinal ridging of the abaxial surface, where it protrudes distally. Towards the cone apex the bracts and fertile scales diminish rapidly in size (Pl. 6, fig. 56), the topmost members being sterile (cf. series of sections V. 30965, V. 30968). In some cones there is a markedly acute tip (Pl. 6, fig. 56), in others it is more blunt (Pl. 6, fig. 55). Only two specimens among the cones have been found attached to their pedicels: Pl. 6, fig. 62, shows one of these, and clothing the pedicel is an overlapping spiral series of broad, flat, lanceolate leaves, as seen in more detail in Pl. 6, fig. 64. These leaves are regularly striated on the abaxial surface; the furrows may represent the position of lines of stomata, but it has not been possible to verify this from structural detail in either sections or cuticles. Another feature of some diagnostic interest is also illustrated by this specimen: it shows a sharp transition from the sterile leaves to the bracts and fertile scales at the base of the cone, a character noted, for example, by Seward & Ford (1906 : 354) as one offering a marked distinction between the Araucariaceae and the Pinaceae, the transition in the former being much more gradual.

The narrow cone axis is seen in transverse section of the basal region of a cone in Pl. 7, fig. 65, and shows a relatively narrow pith and thick cylinder of xylem : the xylem diminishes in thickness towards the tip of the cone. The pith includes large scattered cells with dark brown contents : the stele is endarch, with scanty primary xylem and a wide zone of secondary xylem with regular radial files of tracheids, without parenchyma and without resin ducts or cells, and with unseriate secondary medullary rays. The structure of the xylem is illustrated in more detail in Pl. 7, figs. 66–72. The centrifugal succession of elements in the primary xylem is shown in radial longitudinal section from right to left in Pl. 7, figs 66–68. Annular tracheids cannot be identified with certainty ; but a succession of spiral elements, in which there is some evidence for the formation of bordered pits between the turns of the spiral band (Pl. 7, fig. 67, *s.p.*), is followed by widely reticulate tracheids (Pl. 7, fig. 67, *ret.*) and these are succeeded, in the base of the cone, by tracheids with biseriate alternating bordered pits (Pl. 7, figs. 70, 71, *bi.*), probably belonging to the secondary xylem.

Beyond these come the tracheids forming the bulk of the woody cylinder ; these have uniseriate bordered pits on the radial walls (Pl. 7, figs. 68, 69, 70, *sec.*). The pits are usually contiguous, with flattening of the pit outline in the area of contact (fig. 69) : the form of the pit apertures varies from rounded to oval. Parts of the medullary rays are seen in radial longitudinal section in Pl. 7, figs. 68—70, 72 (*m.r.*) The rays are 1–5 cells high and ray tracheids have not been observed. The cross-field pitting is fairly constant (Pl. 7, fig. 72), there being 2–4 horizontal rows of rather small pits, which are of markedly " cupressoid " form (cf. Phillips, 1941: 267).

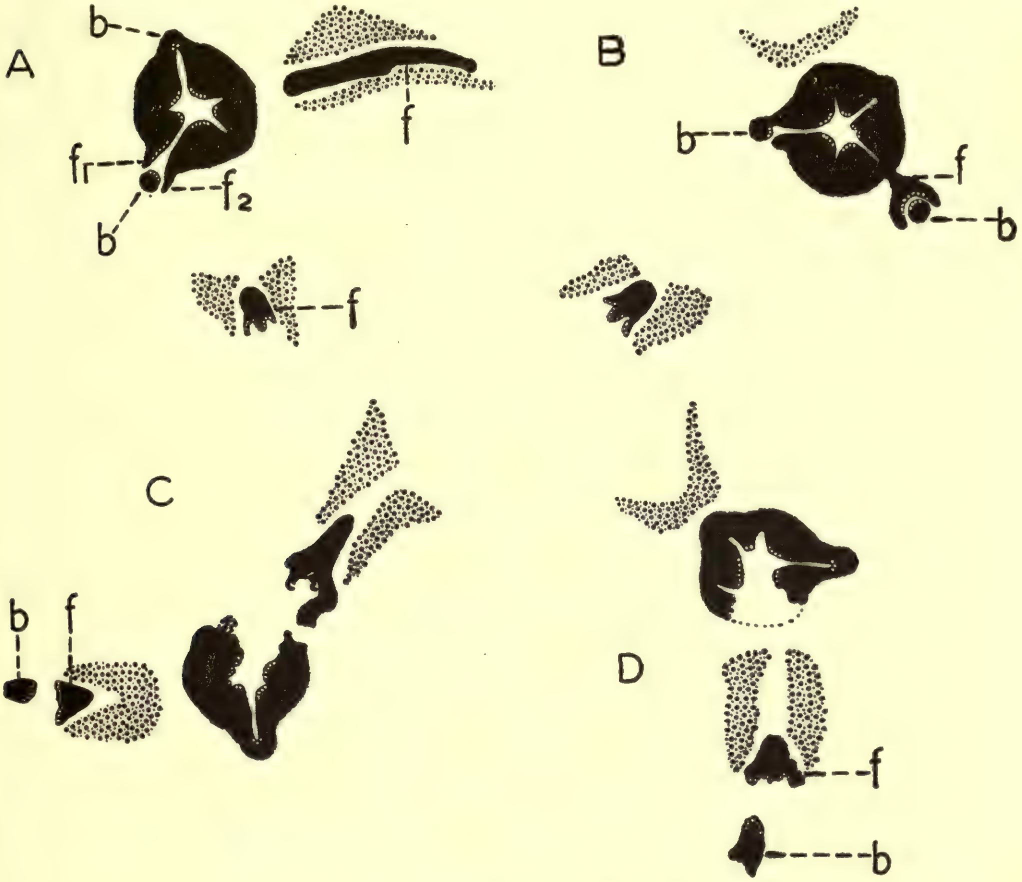
These characters of the xylem, not noted by Wieland, may most conveniently be discussed here : they represent features which have been widely used in the past as a means of identifying conifer woods.

Bailey has recently re-emphasized the comparative significance of the primary developmental succession in the xylem of gymnosperms (Bailey, 1949, 1925 ; cf. also Florin 1936, 1937) ; and in *Pararaucaria* the sequence which has just been noted appears to be intermediate between that found in the " lower " gymnosperms (Cycadales, Cordaitales) and that in the " higher " gymnosperms (Coniferales, Ginkgoales, Gnetales). In the former groups scalariform elements are present and are succeeded by reticulate elements, and these by elements with the typical bordered pits of the metaxylem and secondary xylem ; bordered pits are not formed in the spiral tracheids, where, however, they do appear in the shortened succession found in the xylem of the latter groups, where scalariform and reticulate forms are usually absent. In *Pararaucaria* the presence of reticulate tracheids in the succession is comparable with the similar condition noted by Bailey (1925 : 593) as occurring sporadically in *Araucaria* and *Agathis*, which he has interpreted as intermediate between " lower " and " higher " gymnosperms in this respect. Though it is true that Bailey's observations were made on stem wood and the condition in *Pararaucaria* is reported from the cone axis only the comparison is worth recording, though fuller knowledge of developmental sequence in the cone axes of the various groups is not available for comparison.

The structure of the secondary xylem, in particular the radial pitting of the tracheid walls and the cross-field pitting of the secondary medullary rays, has often been used as a comparative basis for assessing relationships in coniferales. The variability in form and arrangement of tracheid pitting which has been demonstrated in stem and root wood in individual plants in a variety of families of the Coniferales is, however, such that the xylem type in the *Pararaucaria* cones might be included within the range found, for example, in *Pinus*, *Sequoia*, or Araucariaceae (Bailey, 1933 ; Bailey & Faull, 1934 ; Pool, 1929). Cross-field pitting in stem and root wood is also a variable character (e.g., Bannan, 1944). Cupressoid form of the pits in the cross-field is found fairly regularly in the Araucariaceae and Cupressaceae, and it also occurs amongst the Podocarpaceae, Taxodiaceae, Taxaceae, and even occasionally in the Pinaceae (cf. Phillips, 1941 : 268, 274–277). The condition in the Araucariaceae and in *Taxodium*, where the cupressoid cross-field pits may be as numerous as in *Pararaucaria*, probably conforms most nearly with that in the fossil cones. But details of cone-axis wood are available for comparison in very few cases : in *Araucaria* the records given by Thomson (1913, pl. 4, fig. 34) are of multiseriate pitting of the radial tracheid walls of typical araucarian form. This, together with the very wide pith and narrow ring of xylem (Thomson, 1913 : 4, pl. 1, figs. 5, 7) serves readily to distinguish araucarian cone axes from those of *Pararaucaria*. No satisfactory direct comparison with cone axis structure of other families of conifers can be made without further investigation of these. The evidence of the cross-field pitting taken from stem wood structure would, however, tend to favour a reference of the fossil cones to relationship with the Taxodiaceae, where too the same type of tracheidal pitting has been demonstrated in the root of *Sequoia sempervirens* (Bailey & Faull, 1934, pl. 103, fig. 29). [See note on p. 138].

The mode of attachment of the vascular supply of the bract and fertile scale to the axis stele is illustrated in Text-fig. 5, A–D, which is taken from a series of sections at intervals of approximately 2·5 mm. apart, in the basal half of a cone, and viewed from the base upwards. It has not been possible to follow out the course of the bundles from a series through a single leaf-gap : but the vascular supply may be interpreted from a number of gaps cut at varying levels. The bract supply (*b*) comes from the base of the leaf-gap as a single strand, being separate in origin from the supply of the fertile scale, which is derived as two separate strands (Text-fig. 5A, $f^1$, $f^2$,) from the sides of the gap above the bract supply ; these two strands subsequently fuse to give one large bundle (Text-fig. 5, B–D, *f*) after each has undergone torsion through 180°, so that the protoxylem comes to lie on the outer (abaxial) face of the fusion bundle (*f*), which is thus inverted alongside the bract supply (*b*) in the cortex ; the phloem is not preserved. This is also illustrated in Pl. 6, figs. 57, 58, (*b.s.*, *f.s.*). A striking feature, though of subsidiary comparative interest, is the bulky strand of sclerenchyma which accompanies the inverted vascular supply of the fertile scale on its adaxial face (Pl. 6, figs 57, 58, *sc.* ; Text-fig. 5, stippling). This strand, which has its origin in the cortex in the angle above the leaf-gap, forks into two as the fusion bundle passes out of the cortex into the base of the fertile scale, and the paired strands remain a prominent feature in the fertile scale for about half its length (Text-fig. 6).

This account of the origin of the bract and fertile scale supplies does not agree with that of Wieland. He has described, from cut surfaces of cones, the origin of the bract-fertile scale supply as a " single heavy concentric strand " (1935 : 22, pl. 4, fig. 3 ; pl. 5, fig 5). He nevertheless interpreted this condition as being in exact agreement with that in *Pinus*, where however, according to the account of Aase (1915), the bract trace is normally in its origin quite free (except at the cone base) from the fertile scale supply, as indeed is the case in others of the Pinaceae which have been examined (e.g., Aase, 1915 ; Radais, 1894). According to the observa-

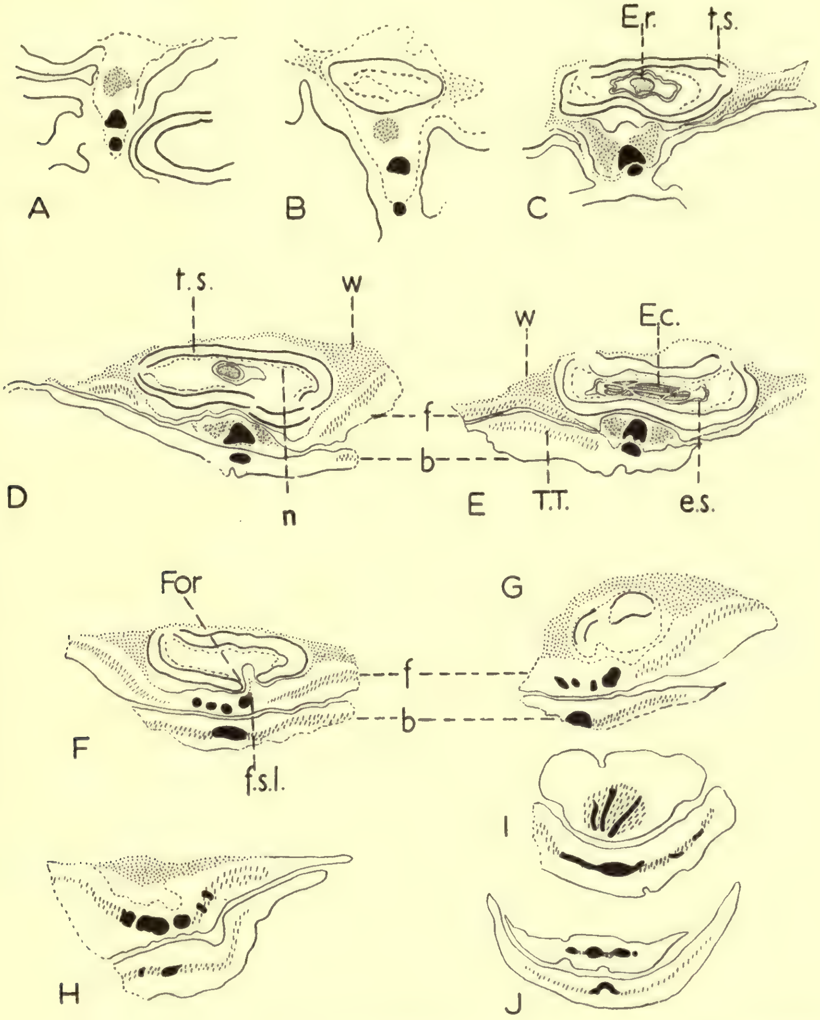


TEXT-FIG. 5. *Pararaucaria patagonica* Wieland. Transverse sections of stele of cone axis from below upwards, to show detachment of bract supply (*b*) and fertile scale supply (*f*1, *f*2), from leaf-gaps. The two traces *f*1, *f*2 of the fertile scale supply fuse with inversion to give a single bundle (*f*). Xylem black, with protoxylem white; sclerenchyma of fertile scale in double stippling. V. 30964 *c–f*. × 6·7.

tions on which the present description is based, *Pararaucaria* does resemble the Pinaceae in this respect, as also the section *Bunya* of *Araucaria*, and some of the Taxodiaceae (Aase, 1915 : 294–7) ; and it has not been possible to confirm Wieland's observations. In his pl. 4, fig. 3, the supplies to the bract and fertile scale are clearly separate but in his pl. 5, fig. 5, there is some evidence that a single strand is present in the cortex outside the leaf-gap : this latter condition, however, is in the cone base, and such a condition has been noted by Aase (1915 : 282–5, 296) as occurring in the base of *Pinus* and *Cryptomeria* cones, though the normal condition higher up is to find the bract and fertile scale supplies quite separate in origin.

The external features of the bract and fertile scale at the cone surface have already been noted : Pl. 6, figs. 57–60 and Text-fig. 6 show their structure in series of tangential longitudinal sections in sequence from inside outwards. The most conspicuous characters are the thick, persistent and probably woody bract (*b*), subtending the thick woody fertile scale (*f*), which bears on its upper surface a single large, inverted seed, which is flattened and winged. The bract is free from the fertile scale for the greater part of its length, and is fused with it only towards the base (Pl. 6, figs. 57–60 and Text-fig. 6). Here the double vascular supply, with the upper bundle (*f.s.*) inverted and accompanied by the two strands of sclerenchyma, is a prominent feature. The lower bundle, which supplies the bract, is single below but forks about half way up the free part of the bract, and the thick, protruding tip of the latter is supplied by a number of small vascular strands linked tangentially by a bulky tissue composed of isodiametric pitted cells, which may be described as a transfusion tissue (Pl. 6, figs. 59, 60, and Text-fig. 6, TT). A curious feature of the bract as described by Wieland was that it was "pleated" (Wieland, 1935, pl. 4, figs. 4, 5). His illustrations show this in respect of one flank only of the bracts, and not in all of them. Closer examination of his figures and of the sections of the series here described has provided evidence (cf. Pl. 6, fig. 57) that this apparent lateral forking or pleating is found only in the bracts cut in inner tangential planes just outside the region where they are attached to the outer cortex of the axis. Here they are so close-set that the margins of their bases tend to be laterally confluent where they overlap, so that a kind of reticulum is formed on the surface of the axis. This is not necessarily a characteristic feature, but one correlated with the closely imbricate succession of the bracts : it is certainly not one characteristic of the free distal region of the bract.

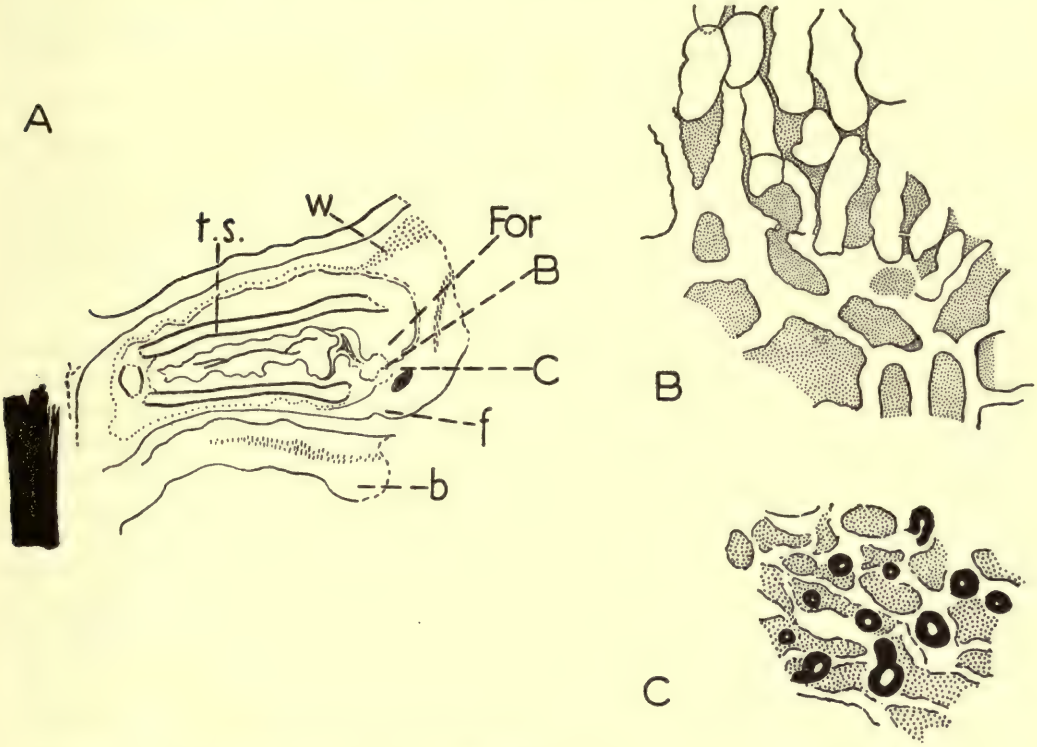
The fertile scale (*f*) is of similar size and thickness to the bract, and is also supplied in its basal region by a single vascular strand (*f.s.*) which remains unbranched until a short distance behind the distal attachment of the seed to the scale. Here it forks into 3–4 strands, and one of these, a lateral strand, passes up to supply the seed in the region of the basal foramen (Pl. 6, fig. 59, and Text-fig. 6F, *f.s.l.*). Above the insertion of the seed the vascular strands supply the prominent tip of the fertile scale ; and here too there is a well-marked transfusion tissue as in the bract. The conspicuous strands of sclerenchyma noted in the base of the fertile scale fade out about half-way up the scale : their function may have been connected with the separation of the seed scales at maturity to liberate the seeds. Though the epidermal and hypodermal tissues of the scale in this region are poorly preserved, there is some evidence (Pl. 6, fig. 60, and Text-fig. 6H) of a grooved abaxial surface on the exposed distal face of the scale, possibly a natural feature, and one which has been noted externally as giving a longitudinally ridged appearance in a few of the best preserved cones (Pl. 6, fig. 63).



TEXT-FIG. 6. *Pararaucaria patagonica* Wieland (cf. Pl. 6, figs. 57–60). Tangential longitudinal sections of fertile scales (*f*) with seed, and bracts (*b*), taken from base outwards. (J = transverse section.) Xylem black, sclerenchyma of fertile scale double stippled, stellate sclerotic wing tissue (*w*) of testa single stippled, transfusion tissue (*TT*) stroked. *For.* = foramen of seed, *fsl* = lateral bundle of fertile scale supplying seed, *ts* = stony later of testa, *Er* = radicle of embryo, *Ec* = cotyledons of embryo, *e.s.* = ? embryo sac, *n* = ? nucellus. (A, B, V. 30959 *c*, *e* ; C–G, V. 30961 ; H, I, V. 30960*a* ; J, V. 30945*a*). × 5.

The seeds themselves are large and flattened ; the latter feature appears to be general and may be a natural character. The usual condition is to find one seed per scale, inverted and with its basal attachment and vascular supply lateral as shown in Pl. 6, fig. 59 and Text-fig. 6F. Wieland reported one cone only in part of which he found 2 seeds per scale, but this condition appears to be exceptional (Wieland, 1935 : 22). All the cones examined appear to be mature ; fully formed embryos are found preserved in the seeds of some of the cones sectioned, and the micropyles, directed towards the cone axis, are sealed (Pl. 7, fig. 73). The seeds at first sight appear to be embedded in the tissue of the fertile scale on its upper surface ; but closer examination shows that this is not the case. There is a conspicuous " stony " layer in the testa (Pl. 6, figs. 57–59, Text-fig. 6, *t.s.*), consisting of a deep zone of elongate, thick-walled cells lying with their longer axes at right angles to the surface. This layer is continuous except for the basal foramen in the region where the seed is attached. The stony layer is surrounded by an outer layer, confluent on either side of the seed body with a flattened wing (Pl. 6, figs. 57–60 and Text-fig. 6, *w*), which consists of a characteristic lacunar tissue of stellate, thick-walled cells or sclereids (Pl. 6, fig. 61), like the " cellules étoilées " of Radais (1894 : 231) in his description of the wings on the seeds of *Abies*. This tissue, resembling an aerenchyma, is markedly different from the tissue of the fertile scale below, to which it is closely adpressed. It corresponds exactly with the tissue described by Radais (1894 : 231, pl. 4, fig. 47) and von Tubeuf (1892 : 205, text-fig. 18) in the wings of the seeds of the Pinaceae, where, in the earlier stages of development, the whole of the inner surface of the seed, including the wing, is attached to the upper surface of the fertile scale, and separation only takes place at a later stage as the seed matures. The evidence from the specimens of *Pararaucaria* here examined, which have all been mature, suggests that the seed, including the wing, is separate from the surface of the scale, except in the region of attachment at the basal foramen (Pl. 6, figs. 57–59 and Text-fig. 6). Text-fig. 7 illustrates the relationship of the seed to the scale in this region : and it can be seen that there is an " absciss " zone here consisting of an aerenchyma-like tissue continuous into the foramen, suggesting that at maturity there is rupture of the tissue in this stalk-like region. This rupture would finally liberate the ripe seed. Without younger stages, it is hardly possible to decide whether the outermost " wing " of the seed coat is at an earlier stage attached to the scale, as in the living Pinaceae, or free from it, as in the living *Agathis* (where the single seed is median) and some of the Taxodiaceae with inverted winged seeds (*Taiwania, Taxodium*). This point, though a critical one, must remain undecided. Wieland's specimens were probably also mature and clearly show the separation of this wing (Wieland, 1935, pl. 4, fig. 5, pl. 5, fig. 2) which he did not recognize when he interpreted the condition of the seeds as comparable with that in *Araucaria*, "inclosed by the drooping curtain-like, expanded, and flattened and coalesced tip of the seed scale" (p. 22). It was principally on the basis of this feature, associated with the *single* seed, that he drew his comparison with the genus *Araucaria*, and instituted the name "*Pararaucaria*" to emphasize the intermediate nature of the genus; for he interpreted the slender cone axis and narrow pith as pinacean characters, together with the more or less free bract (p. 23). Florin, however, described Wieland's "curtain-like" structure as the sarcotesta of the seed coat (1944 : 513), though he did not recognize the seed as winged.

The tissues of the seed inside the stony layer of the testa are poorly preserved in most specimens: but Pl. 6, figs. 57, 58 and Text-fig. 6, C, E, illustrate a cone in which embryos were preserved. The remains of the embryo sac are probably represented at *e.s.*, and of the nucellus at *n*. The embryo is seen cut transversely in the region of the radicle towards the micropylar end of the seed in Pl. 6, fig. 57. and Text-fig. 6, C, and in the region of the cotyledons, towards the base of the seed, in Pl. 6, fig. 58, Text-fig. 6, E. There are several (probably eight) cotyledons. Pl. 7, figs. 73, 75 show an embryo in radial longitudinal section in another cone, with the radicle tip (*r*) pointing towards the sealed micropyle (*m*). This is the only specimen in which it has been possible to demonstrate an embryo in median longitudinal section



TEXT-FIG. 7. *Pararaucaria patagonica* Wieland. A. Longitudinal section of fertile scale (*f*) and bract (*b*) of cone, cut to one side of median plane to show foramen of seed (*For.*) in region of attachment to scale. *ts* = stony layer of testa, *w* = wing tissue of testa: xylem of cone axis and fertile scale shown in black. V. 30966*a*. × 6·7. B. Tissue shown at *B* in foramen of seed in fig. A. × 240. C. Tissue shown at *C* in fig. A. × 240. In B and C, intercellular spaces stippled, thick-walled ? fibrous cells in solid black.

to confirm the orientation. In Wieland's account (1935 : 22) he refers to a suggestion of a dicotyledonous embryo, but the preservation of his specimens left this point inconclusive.

Butts & Buchholz (1940) have shown that in the Pinaceae, polycotyledonary embryos with cotyledons reaching nine in number are a characteristic feature, while in the Taxodiaceae, the number varies among the genera from 8 to 2. But in the remaining families of the conifers embryos with 3 or more cotyledons do occur in certain genera, though the usual number is 2, so that the character has a limited diagnostic value.

## RELATIONSHIPS

The chief features of *Pararaucaria patagonica* here described which were not noted by Wieland (1935) in his account of the species are: the foliation of the pedicel; the details of the wood structure; the detachment of the bract trace from the cone stele separately from the two traces which form the supply of the fertile scale; the winged, detachable nature of the inverted seed and its lateral position; and the polycotyledonary embryo.

Wieland's account established the characters of slender cone axis with narrow pith, and the conspicuous bract scales of the cone bearing in their axils the large fertile scales each normally with one large inverted seed, which he interpreted as being enclosed in the scale tissue. On this association of characters he assessed the systematic position of the genus as intermediate between Pinaceae and *Araucaria* (Wieland, 1935 : 23), and accordingly instituted the generic name *Pararaucaria.* A re-analysis of the relationships of the genus is attempted in the following table on the basis of the fuller set of criteria of comparison which can now be used. The available characters of the petrified cones which might be suitable for giving a quantitative index of aggregate intergeneric differences are too few in number for effective use: but the table summarizes the position qualitatively.

### *Pararaucaria patagonica* Wieland, emend.

*List of Characters used for Comparison with some other Coniferales, Numbered for Reference as in Table below.*

1. Bract free from fertile scale for greater part of length.
2. Bract large and conspicuous at maturity.
3. Bract trace distinct in origin from traces of fertile scale.
4. Usually one seed per fertile scale.
5. Seeds inverted.
6. Seeds attached laterally.
7. Seeds winged.
8. Seeds free throughout development from fertile scale, except in region of basal foramen.
9. Several cotyledons ($> 4$) in embryo of seed.
10. Cone axis slender, with narrow pith in stele.
11. Secondary medullary rays of cone axis wood with pits of cross-field cupressoid and numerous.

## TABLE SHOWING POSITIVE CORRELATIONS WITH SOME FAMILIES AND GENERA OF CONIFERALES.

Characters compared numbered as in list above.
+ = positive correlation in all species described.
⊕ = positive correlation in some species described.
? = doubtful or undescribed character.

| | Characters of bract, fertile scale and seed. | | | | | | | | | Cone axis | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1. | 2. | 3. | 4. | 5. | 6. | 7. | 8. | 9. | 10. | 11. |
| *Pararaucaria* | + | + | + | + | + | + | + | ? | + | + | + |
| *Araucaria* | .. | + | ⊕ | + | + | ? | .. | .. | .. | .. | + |
| *Agathis* | .. | + | .. | + | + | .. | + | + | .. | .. | + |
| Pinaceae | + | .. | + | .. | + | + | + | .. | + | + | .. |
| Taxodiaceae | .. | + | ⊕ | .. | ⊕ | + | ⊕ | + | ⊕ | + | ⊕ |
| **Romeroites* | .. | + | ? | .. | .. | ? | .. | + | ? | + | ? |
| *Cheirolepidaceae | ⊕ | ⊕ | ? | .. | + | + | .. | .. | ? | ? | ? |
| **Pseudo-Araucaria* | .. | ? | ? | .. | ? | + | .. | .. | ? | ? | ? |

* The data for these fossils, which superficially bear some resemblance to *Pararaucaria*, are taken from the accounts given by Spegazzini (1924: *Romeroites*), Hirmer & Hörhammer (1934: Cheirolepidaceae), Fliche (1895: *Pseudo-Araucaria*). A revision of the characters in all these types, especially of the relationship between seed and fertile scale, is necessary before any critical systematic comparison with *Pararaucaria* can be made.

It will be seen on summation of positive correlations that the nearest comparison is with the Taxodiaceae (*sensu* Pilger, 1926 : 342), which shows the greatest number of positive correlations. Even allowing for uncertainty on criterion (8) in *Pararaucaria* (freedom of seed from scale throughout development), the comparison with the Taxodiaceae is closer than with the Pinaceae, for on criteria (2) and (11) (large size of bract; and cross-field pits numerous, cupressoid) the conditions found in *Pararaucaria* and amongst the Taxodiaceae do not characterize the Pinaceae: and on criteria (1) and (4) (degree of freedom of bract from fertile scale, and number of seeds per scale), which represent the chief differences between *Pararaucaria* and the Taxodiaceae, it may be noted on (1) that in *Cryptomeria* (and probably also in the Jurassic genus *Elatides*) in the Taxodiaceae there is a form intermediate in respect of degree of fusion of bract and fertile scale, and on (4), that in *Taiwania* in the Taxodiaceae a single seed instead of two may sometimes be found, while in *Pararaucaria* the two-seeded condition has abnormally been found. In these two respects *Cryptomeria* and *Taiwania* respectively may be regarded as intermediate between the *Pararaucaria* condition and a more typical taxodiaceous condition.

Certain features of *Pararaucaria* have been omitted from the lists above as not affording sufficiently reliable distinctions: these are the foliation of the pedicel, the sharp transition from the foliation of the pedicel to the bracts and fertile scales of the cone itself, the size of the cones and the number of cone-scales per cone, the radial pitting of the tracheid walls, and the vertical ridging of the fertile scales. But it may be noted that in each of these features correspondence with characters occurring amongst the Taxodiaceae may be found. In the case of the radial pitting of the tracheids, reference may be made to the range of variability in xylem structure demonstrated in the Redwood, *Sequoia sempervirens*, by Bailey & Faull (1934, pl. 103, fig. 29), where the condition in the fossil cones is found in secondary xylem of root. The vertical ridging of the fertile scale is, so far as I am aware, a feature characteristic of the Taxodiaceae in the genera *Sequoia*, *Sciadopitys*, and *Taxodium*, though in the first two of these it is also found to some extent in the bract. Finally, the general "habit" of the cones is taxodiaceous ; the proportion of bract to fertile scale, the size of the cones, the vertical ridging of the fertile scale, all combine to give a habit which on superficial examination one would tend to refer to the Taxodiaceae.

In the analyses just given, the Taxodiaceae are referred to in the sense of Pilger's definition (Pilger, 1926 : 347) ; the family in this widely-defined sense shows considerable diversity in certain characters, e.g., the orientation of the seed, and the number of the cotyledons. The probably heterogeneity of the Taxodiaceae in this inclusive sense has, however, been generally recognized : Pilger himself separates the genera into two sub-families and a number of sub-groups, while Hayata (1932) arranged the genera of Pilger's group in a number of separate families. Florin has more recently re-examined the relationships of the Taxodiaceae, *sensu* Pilger, (Florin, 1931 : 484–491 ; 1940 : 78). He agrees (1931 : 490) with Pilger's classification, whilst admitting it may be artificial, since it deals with a family intermediate in its general characters between others more sharply defined : but at the same time he has re-emphasized its diversity and probable heterogeneity. In particular, he draws attention, amongst other distinctive features, to the characteristic epidermal characters of the Tasmanian genus, *Athrotaxis*, which can readily be used to distinguish it from other genera of Taxodiaceae in the northern hemisphere.

In view of this diversity in the Taxodiaceae, *sensu latu*, *Pararaucaria* may meantime most conveniently be referred to this family. It most nearly resembles *Taiwania* in the one-seeded condition, *Cryptomeria* in the condition of the bract in relation to fertile scale, and *Sequoia* and *Taxodium* in the polycotyledonary embryo, but resembles no one living genus in its combination of characters. The possibility remains, however, that the seed and its wing may have been attached, in earlier stages of development, to the fertile scale as in the Pinaceae : and in this case the most natural position would be to place *Pararaucaria* in a separate new family of Coniferales, intermediate in position between the Taxodiaceae and Pinaceae. In a recent review by Takhtajan (1953) the phylogeny of the Taxodiaceae has again been discussed, and he suggests that they probably originated from the earliest and most primitive Pinaceae, though no fresh evidence is adduced in support of this view.

Wieland (1935 : 24) referred *Pararaucaria* to the fossil family Cheirolepidaceae as defined by Hirmer & Hörhammer (1934 : 79) : but this reference was based on the assumption that the seed was borne in the scale tissue as in the genus *Araucaria*, and as has already been demonstrated, this is not the case. Florin (1940 : 36 ; 1944 : 513) suggested that *Pararaucaria* might be identical with the South American fossil genus *Romeroites*, from the province of Neuquen. This genus, as described by Spegazzini (1924 : 134), is undoubtedly taxodiaceous, but differs from *Pararaucaria* chiefly in the thin, many-seeded fertile scales with seeds upright and fleshy, and fusion of bract with fertile scale for the greater part of its length. A more detailed description of this genus is undoubtedly desirable, but according to Spegazzini's account it does not correspond with *Pararaucaria*, though the size of the cones and the general external habit are somewhat similar. Gothan (1950 : 153) in a very brief note recognized that *Pararaucaria* had nothing to do with *Araucaria*, and accordingly indicated that the genus was misnamed: but he gave no further description of the cones nor indication of their true relationships, of which, as has been shown, no more satisfactory definition can be given unless younger stages in the development of the cones are found.

## DISCUSSION

The chief interest of these conifers of the Cerro Cuadrado forest lies in their relationship with other conifers and their geographical distribution.

*Araucaria mirabilis* is an extinct species, and appears to have its nearest living relation in the Queensland " bunya bunya," *A. bidwilli*, and not in *A. araucana* or *A. angustifolia*, the only living species of *Araucaria* in South America ; but it might be considered to represent an ancestral form of these, if the wings of the cone scales had become reduced in the evolution of the species. This view on the evolution of the South American living araucarians has already been expressed by Darrow (1936 : 333). The South American fossil records (cf. Florin's review, 1940 : 33–40) do not include any which furnish critical evidence of the wingless cone scales of species of the section *Columbea* Endlicher, emend. Wilde & Eames : the cone scale from the (?) Upper Cretaceous of the Cerro Guido in Santa Cruz, which was named *Araucarites patagonica* by Kurtz (1902 : 49) and referred to as comparable with the living *Araucaria brasiliensis*, was not figured, and was an incomplete specimen described as representing the lower part of the scale. Other cone scales in the form of compressions, from Meseta de Baquero in Santa Cruz, have also been referred to the section *Columbea* (Feruglio, 1951 : 65). These are more or less incomplete and are not illustrated, but from the description and from their comparison by Feruglio with Berry's cone scales of *Araucaria* from the nearby Gran Bajo de San Julian (Berry, 1924 : 480, text-figs. 2, 2*a*) it appears that they are winged scales. Berry refers to his as " obviously thick and woody," which suggests that they may have belonged to the section *Bunya* Wilde & Eames though they are much smaller than those of the living *A. bidwilli*. Other seed scales, which he also compared with Berry's, were described by Feruglio as *Araucaria* (Feruglio, 1951 : 39), from the Gran Bajo de San Julian, and they too might have belonged to the section *Bunya*. Both Berry's and Feruglio's seed scales come from localities in the region of the same volcanic complex (the porphyritic series of the Bahia Laura), which Feruglio has dated as of age mid-Jurassic to Wealden (1951 : 74), and which also contains the petrified forest around the Cerro Alto ; but it is unlikely, owing to the incomplete preservation of the compressed cone scales, that any close comparison can be made between them and the petrified cone scales of *Araucaria mirabilis* in the forest, though they are not dissimilar in size and general form. Feruglio does not believe that the San Julian specimens are identical with *Araucaria mirabilis*.

There is, therefore, as yet no critical record of wingless cone scales in South American fossil floras. The evidence so far provided from sterile shoots with broad flat leaves might indicate araucarians of the sections *Bunya* Wilde & Eames, *Intermedia* White, or *Columbea* Endlicher emend. Wilde & Eames; and petrified woods have not yet provided reliable evidence for distinction of these sections. The South American records are, however, relatively scanty, and the absence from them of critical evidence of fossil species of *Columbea, sensu* Wilde & Eames, is necessarily inconclusive for assessment of the age of this section on the South American continent in comparison with that of species of the section *Bunya*, of which *A. mirabilis* is the only fossil form with critical structural evidence of relationship. Wingless araucarian cone scales are rare in the fossil records of the Southern Hemisphere as a whole (Florin, 1940 : 27), but they have been reported from the Jurassic of Australia and New Zealand (*A. grandis* Walkom, 1921 : 13, pl, 3, fig. 6 ; Edwards, 1934 : 100), suggesting that they may have been as ancient as the winged types, which are abundant in Jurassic rocks, and indicating that they did occur in Mesozoic times in Australasia, where they are now extinct The evidence, therefore, though scanty, does not support the attractive hypothesis of the South American evolution of *Columbea*; and accordingly, *A. mirabilis* probably bears no direct relationship to the living South American species, but represents an extinct element of an earlier more widespread araucarian flora, some of the species of which have disappeared. The presence of such a type as *A. mirabilis* in South America, however, does provide another link between the floras of Australasia and South America. *A. mirabilis* may well have been a member of the parent stock from which the modern " bunya bunya " of Queensland sprang, a stock more widely spread than its descendents ; but in the development of the South American floras it eventually died out, while the species with wingless cone scales persisted there to the present day. Araucarians belonging to the Australasian sections *Eutacta* or *Intermedia*, with wide, thin, papery wings on the seed scales, were also represented in earlier South American floras ; perhaps the best evidence for this is provided by *Araucaria pichileufensis*, described by Berry from Rio Pichileufu in Territory of Rio Negro (Berry, 1938 : 59, pl. 11, fig. 1). This is a Tertiary species, though its exact age is doubtful (Florin, 1940 : 39), and might suggest that either section *Eutacta* or *Intermedia* persisted longer before extinction on the South American continent than did *Bunya*, though critical records are too scanty for such a generalization to be made at this stage. Florin has renewed the emphasis on the part probably played by Antarctica, whether as an intercontinental land bridge along which migration could take place, or as the place of origin of some of the southern genera (Florin, 1940 : 85–6, 92) : and the distribution of fossil and living species of *Araucaria* in South America and Australasia supports this hypothesis.

*Pararaucaria patagonica* represents an extinct genus and presents a different problem in distribution. The Taxodiaceae, which probably represent the nearest living relations of this genus, are to-day confined to the northern hemisphere, with the exception of *Athrotaxis*, with three species living in Tasmania. The only other fossil records of this family from the southern hemisphere are three species of *Athrotaxis*—*A. ungeri* (Halle) from the Mesozoic (possibly Lower Cretaceous) of Southern

Patagonia, and two other species from the Cretaceous of New Zealand and the Tertiary of Tasmania (Halle, 1913: 40–44; Florin, 1940: 35, 77)—and *Romeroites argentinensis* Speg. (Spegazzini, 1924: 134–9), from Neuquen, South America (? Upper Jurassic or Cretaceous). Florin has, however, drawn attention to the separate and peculiar nature of the genus *Athrotaxis*, and has suggested that it may represent a distinct, though probably remotely related, line of descent from the Taxodiaceae. *Pararaucaria* adds, then, to the evidence for an earlier more widespread distribution of taxodiaceous types of plant in the southern hemisphere; along with *Romeroites*, it is now extinct, while *Athrotaxis* has disappeared from South America. *Pararaucaria* is the only genus related to the Taxodiaceae which shows freedom of bract from fertile scale for the greater part of its length, and so might be regarded as an earlier member of an evolutionary series of forms leading to some of the modern Taxodiaceae where fusion is more or less complete. Such an interpretation would place *Pararaucaria* in line with that of Florin for the evolution of the coniferalean ovulate strobilus, where he regards the cohesion of the bract with its axillary seed scale complex as a condition derivative from more primitive forms where they are free. However, the Taxodiaceae (*sensu* Pilger) are an ancient and widespread family in the northern hemisphere; among living genera, *Sciadopitys* is already known in the Jurassic, and other genera are abundant in younger rocks, especially in the Tertiary. Hirmer has however (1936: 65), also included the much older Upper Permian *Pseudovoltzia*, the Triassic *Voltzia* and the Rhaeto-Liassic *Swedenborgia* in this family: in the two former genera, the bract and ovuliferous scale are more or less free, and in the latter are partially fused. Lack of critical evidence for the exact geological age of *Pararaucaria* precludes close phyletic comparison with other taxodiaceous genera: but as already indicated (p. 102), the most recent evidence places the age of the petrified forest as at some stage between mid-Jurassic and Wealden. The characters of *Pararaucaria* itself certainly support the assignation of Mesozoic rather than Tertiary age, for in younger floras the majority of the genera are modern, and *Pararaucaria* cannot be closely compared with any living genus. A reference made by Wehrfeld (1935) to wood of palms in the Cerro Cuadrado floras has never been substantiated; and the genus *Araucaria*, as represented by the extinct *A. mirabilis* in the same flora, is itself an ancient one, dating back to the Jurassic. It is probable that *Pararaucaria* represents an extinct offshoot from some common earlier stock of the Taxodiaceae, no doubt of northern origin, which underwent separate evolution south of the equator, as suggested by Florin for the case of *Athrotaxis*, rather than a type to be regarded as directly ancestral to any of the living genera.

The unique one-seeded fertile scale of *Pararaucaria* is a striking case of homeotic similarity with the condition found in many other conifers of the southern hemisphere —*Araucaria*, *Agathis*, and the Podocarpaceae, where distribution of the single seed is associated with the entire woody cone-scale, separate winged seed and entire cone-scale with fleshy developments respectively. Biologically, the closest comparison in this respect with *Pararaucaria* is with *Agathis*, where there is also a single winged seed, but with median insertion on a single cone-scale representing the completely fused bract and fertile scale. In the living northern Coniferales (excluding Taxales) the cone-scales are normally two to many-seeded, with detachable seeds, though in the taxodiaceous genus *Taiwania*, which usually has two winged seeds per scale, one of these is frequently missing and the condition is similar to that in *Pararaucaria.* This modern condition in the northern Coniferales is in contrast with that amongst the oldest northern conifer floras of the Upper Carboniferous and Permian, where two of the most widespread genera, *Lebachia* and *Ullmannia*, had one-seeded seed-scale complexes. This condition disappeared relatively early in the history of northern conifers ; though the Araucariaceae are notable exceptions during the Mesozoic in northern lands, they too disappeared from northern floras during early Tertiary times. In any case, this family may have had its origins in the southern continent and have spread northwards, though final proofs of this are lacking (Florin, 1940 : 78–82, 90). However, little is known of the early history of the southern floras ; and in them the one-seeded cone scale may in some cases represent, as seems probable in *Pararaucaria*, the result of reduction in number of seeds on the fertile shoot, rather than the retention of a primitive character.

There is no evidence that the possession of a single seed per seed-scale complex has conferred any special biological advantage amongst southern conifers, except in so far as it has made possible, in the genus *Araucaria*, the distribution of the single seed still associated with the protective cone-scale tissue in fruit-like fashion, simulating the samara or nut of angiosperms ; a somewhat similar condition is found in Podocarpaceae, in association with fleshy developments. In these two families a condition analogous in some respects with angiospermy has thus been attained, and the corresponding increase in degree of protection of the seed might in some measure account for the success of these two families. But in *Agathis* and *Pararaucaria* no such additional protection is associated with the single-seeded habit, though the larger size of the seeds ensured by the reduction in number may have had advantages in germination.

## CONCLUSIONS

According to this interpretation of the remarkable petrified forest of the Cerro Cuadrado region, it is unique in a number of respects amongst other petrified forests. The abundant material of petrified and fertile seed cones of the two dominant types of tree gives a basis for a fairly satisfactory systematic comparison with other living and extinct conifers : the structure of the embryos, for example, and of the vascularization of the cone-scales and ligule in the araucarian cones, are characters which one can hope to demonstrate only very rarely in fossil conifers, and close comparison with living species is impracticable without them. Conclusive evidence of only two species, both based on seed cones, has been found in the forest—*Araucaria mirabilis* ; and *Pararaucaria patagonica*, whose affinities are probably with the Taxodiaceae. The detached portions of wood, branches and twigs most probably belonged to one or other of these species, though critical proof of relationship is lacking. The presence of the numerous petrified seedlings affords a unique demonstration of regeneration, probably of the araucarian species, in the forest. Both the dominant species are extinct, but one, *A. mirabilis*, probably disappeared in the course of evolution of section *Bunya* of the genus *Araucaria*, while the other, *Pararaucaria patagonica*, left no descendants, the family of the Taxodiaceae having disappeared from South America without having played a prominent part in its floras so far as may be judged from the scanty fossil evidence. The characters of *Pararaucaria* in particular suggest an age not younger than Cretaceous for the forest : for no close taxonomic comparison with any living genus can be made.

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Note for p. 122.

The pith structure in the *Pararaucaria* cones resembles quite closely that of the stem in the living *Taiwania cryptomerioides*. Doyle M. H. & Doyle, J. (1948, *Proc. R. Irish Acad.*, **52,** B : 26, text-fig. 5) have demonstrated that the pith structure in stems of Taxodiaceae may be used as a diagnostic character for the genera, though corresponding observations for cone axis anatomy are not available.]

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## DESCRIPTION OF PLATES

All figures are from untouched photographs.

Pl. 1, figs. 1, 4–6, 8–13 ; Pl. 2, figs. 14–20 ; Pl. 3, figs. 26–37 ; Pl. 4, figs. 38–42 ; Pl. 5, fig. 46 ; Pl. 6, figs. 55, 56, 62–64 ; Pl. 7, figs. 74, 75, are taken by reflected light. Pl. 4, fig. 43 and Pl. 5, figs. 50–54 are taken from thin sections against a black background.

The photographs in Pl. 1, figs. 3, 7 ; Pl. 5, figs. 48, 49 ; Pl. 6, fig. 63, and Pl. 7, figs. 66–73 were taken by Mr. E. Ashby, Department of Cryptogamic Botany, University of Manchester.

## PLATE 1

*Araucarites sanctaecrucis* n. sp. and Coniferous Wood.

FIG. 1. Leafy (L) and decorticated (W) branches embedded in matrix. V. 30936. × 0·6.

Coniferous Wood.

FIG. 2. Transverse section of a woody branch, probably 12 years old, showing pith (*p*), annual rings in the secondary xylem (*x*), and remains of cortical tissue (? periderm, *c*). V. 30937*a*. × 0·8.

FIG. 3. Radial longitudinal section of branch seen in fig. 2, showing pitting on radial walls of tracheids. V. 30937*b*. × 250.

*Araucarites sanctaecrucis* n. sp.

FIG. 4. Foliated ? 2-year-old branch, showing lateral branches. V. 30938. × 0·9.

FIG. 5. Detail of abaxial leaf surface from specimen showing grooves and ridges (cf. branch seen in fig. 4). V. 30939. × 15.

FIG. 6. Partially decorticated ? 3-year-old branch with apparent whorl of ? 2-year-old lateral branches. V. 30940. × 0·8.

Coniferous Wood.

FIG. 7. Detail of pitting shown in fig. 3. V. 30937*b*. × 500.

*Araucarites sanctaecrucis* n. sp.

FIG. 8. Transversely cut top end of branch shown in figs. 10, 11, with (? 4) annual rings in the secondary xylem (*x*), and leaf bases (*b*) and leaf tips (*t*) transversely cut. V. 30941. × 1.

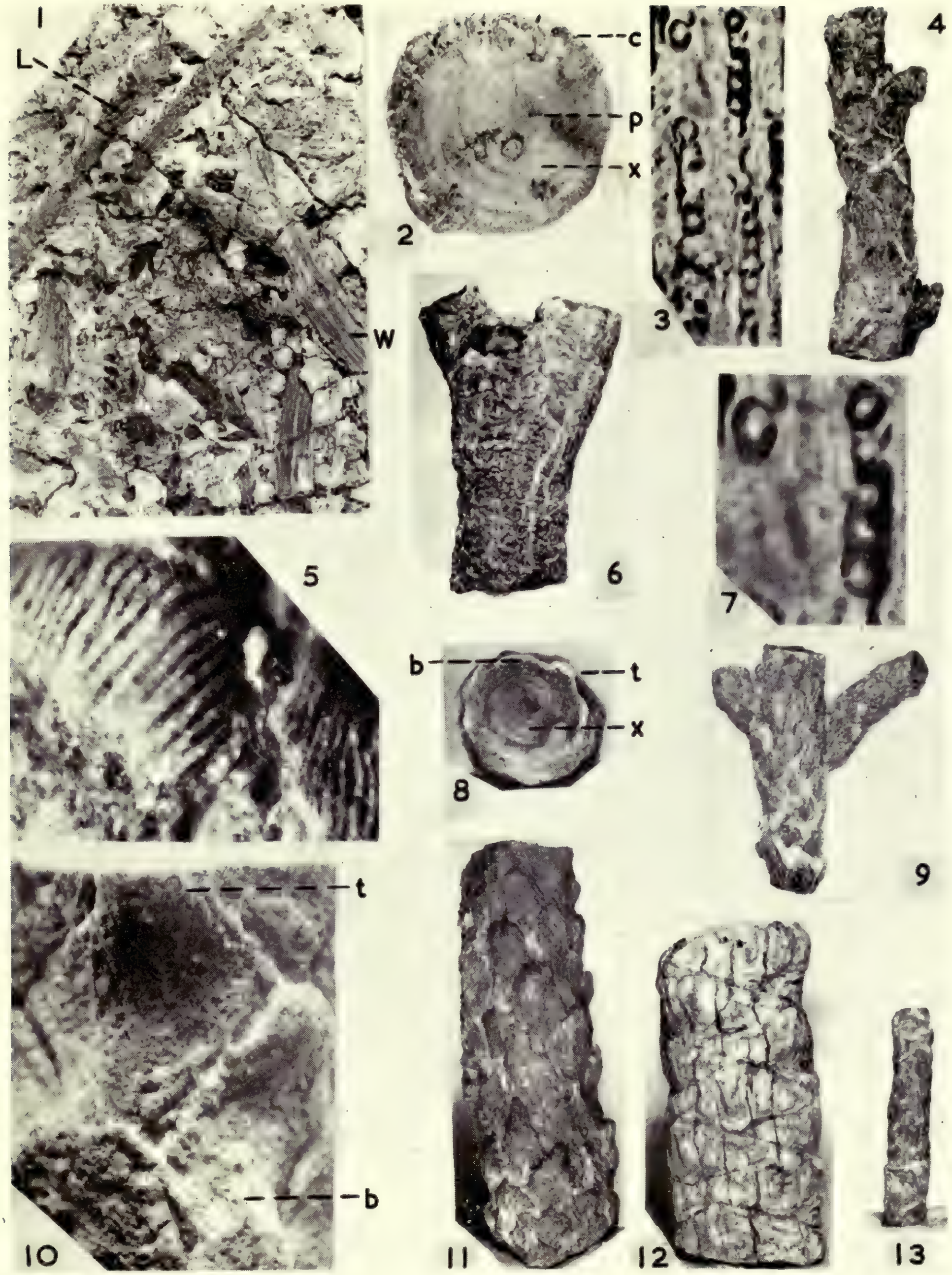
FIG. 9. Leafy 2-year-old branch with one-year-old branches arranged in two ranks. V. 30942. × 0·9.

FIG. 10. Detail of leaves from the top of the branch shown in figs. 8, 11. *b* = leaf base, *t* = leaf tip. V. 30941. × 3·8.

FIG. 11. Leafy branch (? 4-year-old). V. 30941. × 0·8.

FIG. 12. Defoliated branch (? 5-year-old) showing rhomboidal leaf bases. V. 30943. × 0·9.

FIG. 13. 1-year-old leafy branch. V. 30944. × 0·8.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*ARAUCARITES*

## PLATE 2

Seedlings (cf. *Araucaria mirabilis*).

FIG. 14. Broken seedling (*S*), along with separate fragments of branches and twigs, embedded in matrix. V. 30936. × 0·6.

FIGS. 15–17. Broken seedlings of various shapes (see text). V. 30946–48. × 0·9.

FIG. 18. External view of seedling showing periderm (*pd*) and woody core (*x*). V. 30949. × 0·9.

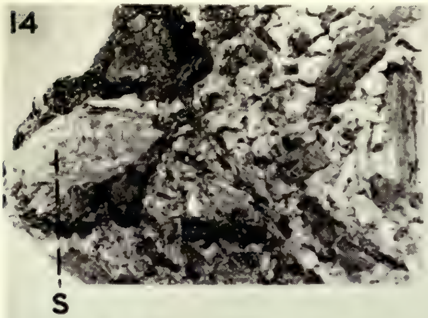
FIG. 19. Median longitudinally-cut surface of half seedling shown in fig. 18. × 0·9.

FIG. 20. Transversely-cut surface of swollen region of seedling similar to those shown in figs. 17, 18. V. 30950. × 0·9.

FIG. 21. Radial longitudinal section of top end of seedling similar to that shown in fig. 15. *p* = pith. V. 30951*a*. × 0·8.

FIG. 22. Transverse section of central swollen region of seedling similar to those shown in figs. 17–20. *pd* = periderm, *x* = secondary xylem. V. 30952*a*. × 0·8.

FIGS. 23–25. Transverse sections through top, middle and basal end respectively of seedling similar to that shown in fig. 15. *p* = pith, *pr* = primary xylem, *x* = secondary xylem (cf. Text-fig. 1). V. 30951*b*–*d*. × 25.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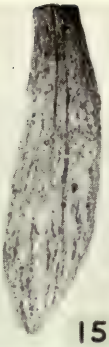
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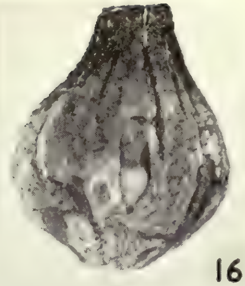
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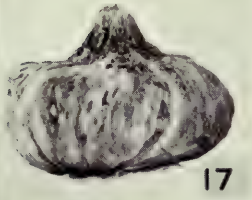
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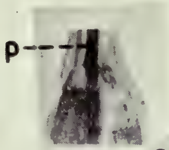

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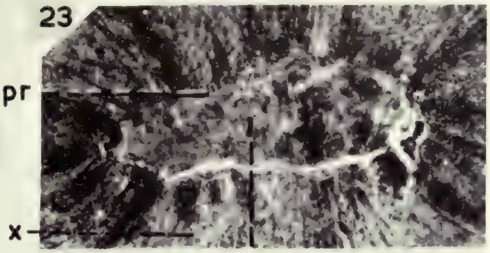
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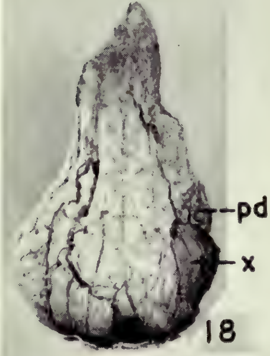

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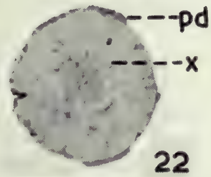

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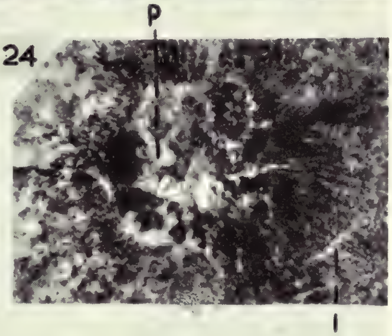
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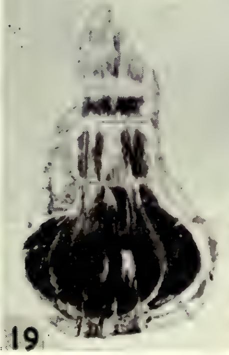
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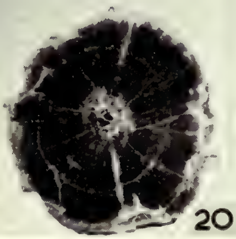
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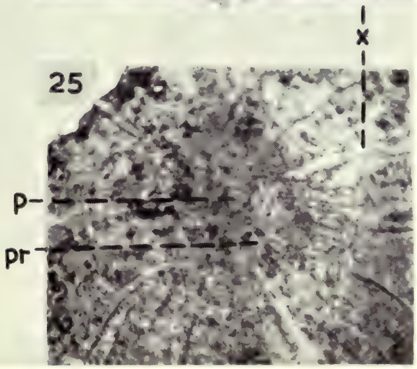
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Araucarian Seedlings

## PLATE 3

*Araucaria mirabilis* (Spegazzini).

FIG. 26. Petrified cones embedded in matrix. V. 30953. × 0·4

FIG. 27. Cone broken transversely half way up axis, showing pith (*p*), vascular bundles (*v*), and cone-scales with seeds (*s*). V. 39054. × 0·9.

FIG. 28. External features of cone shown in fig. 27. *l* = ligule, *a* = apophysis of bract. × 0·9.

FIG. 29. Detail of external features of cone-scales shown in fig. 28. *l* = ligule, *a* = apophysis of bract, *w* = wing. × 4·1.

FIG. 30. Base of cone shown in fig. 35; showing transversely cut pedicel (*pl*), and gradual transition from sterile to fertile scales at base of axis. V. 30955. × 0·8.

FIG. 31. Small cone, showing overlapping laminar tips of bracts. V. 30956. × 0·8.

FIG. 32. Cone shown in fig. 31, median longitudinal surface, showing wide pith (*p*) and immature or sterile cone-scales (*c*). × 0·8.

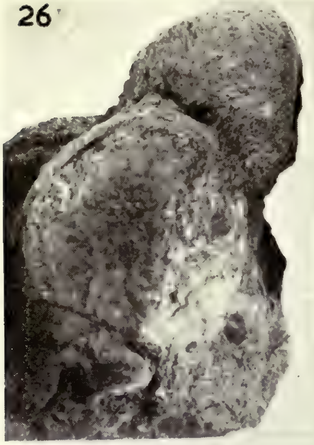
FIG. 33. Detail of cone scales in fig. 32, showing ligule (*l*) and bract (*b*); no ovules have been formed. × 4·1.

FIG. 34. Detail of fig. 31, showing laminar tips of bracts. × 4·1.

FIG. 35. Polished longitudinally cut surface of half cone shown in fig. 30. A = cone-scale shown in detail in figs. 36–37; B = cone-scale cut in approximately median longitudinal section; E = embryo in seed. × 0·9.

FIG. 36. Detail of fig. 35 at A. *l* = ligule, *a* = apophysis of bract (artificially split), *S* = seed (cut to one side of median plane), *l.s.* = ligular sulcus. × 4·1.

FIG. 37. Surface view of half cone-scale shown in section in fig. 36. *l* = ligule, *a* = apophysis of bract. × 4·1.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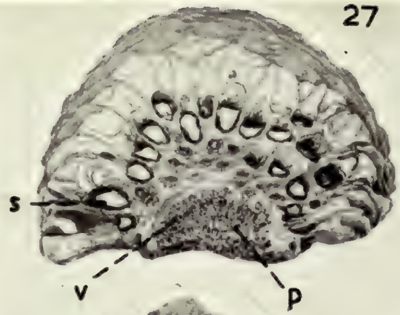
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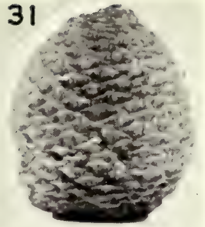
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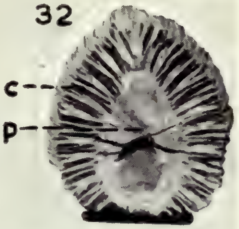
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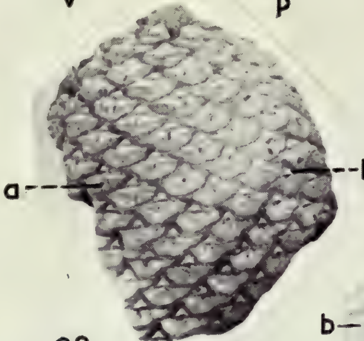
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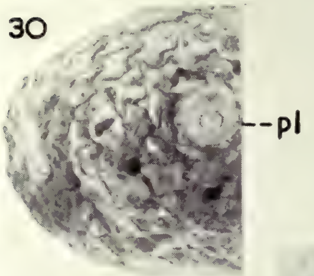
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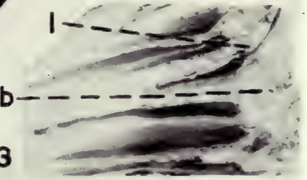
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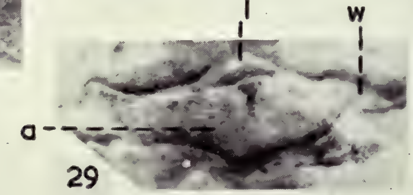
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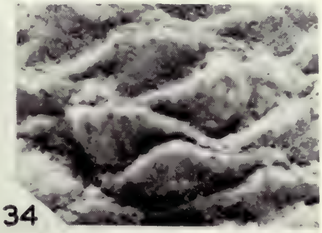
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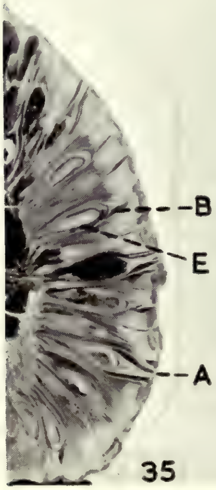
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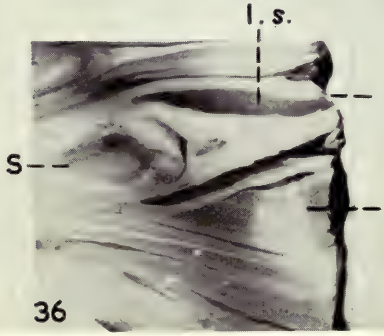
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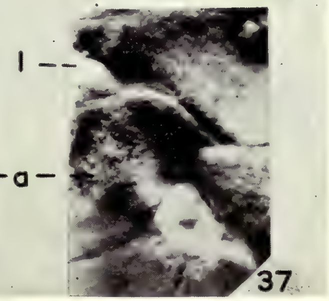
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*ARAUCARIA MIRABILIS*

## PLATE 4

*Araucaria mirabilis* (Spegazzini).

Fig. 38. Half cone in surface view, showing persistent laminar tips of bracts of cone-scales. Structure illustrated in figs. 39–45, and Pl. 5, fig. 54. V. 30957. × 0·8.

Fig. 39. Detail of fig. 38, showing persistent laminar tips of bracts (*t*), with longitudinal striation. × 4·1.

Fig. 40. Detail of median longitudinally cut face at mid left of half cone in fig. 42, with apophysis of bract (*a*), persistent laminar tip of bract (*t*), ligule (*l*), embryo (*e*), (A = ? absciss zone.) × 4·1.

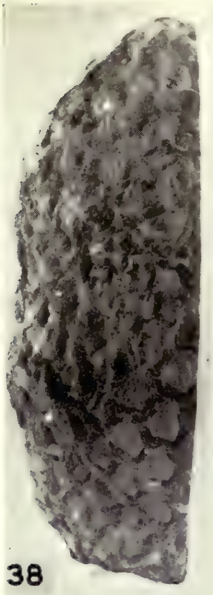
Fig. 41. Detail of embryo from fig. 42, showing two cotyledons. × 4·1.

Fig. 42. Polished median face of half cone shown in fig. 38 ; *p* = pith, *v.b.* = vascular bundles of axis ; details of cone scales in figs. 40, 41. × 0·8.

Fig. 43. Tangential longitudinal section of cone (cf. figs. 38–42), taken at level of persistent laminar tip of bract. *a* = apophysis of bract, *t* = laminar tip, *v.b.b.* = vascular bundles of bract. V. 30957. × 4·1.

Fig. 44. Detail of vascular strand in ligule. *tr* = spiral tracheids. V. 30957. × 208.

Fig. 45. Detail of vascular bundle from persistent laminar tip of bract shown in fig. 43. *d* = ? resin duct, *v.b.* = vascular bundle. × 55.



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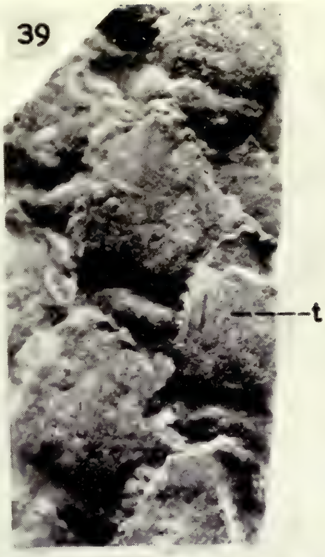

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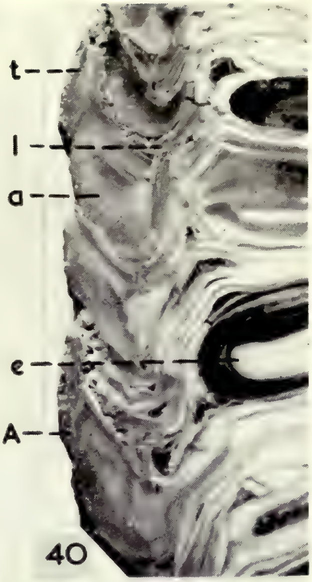

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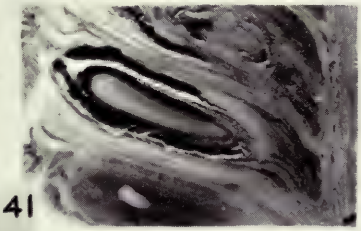

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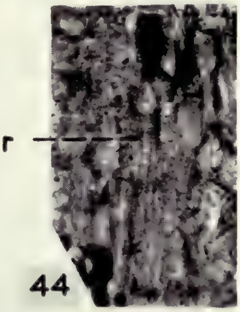

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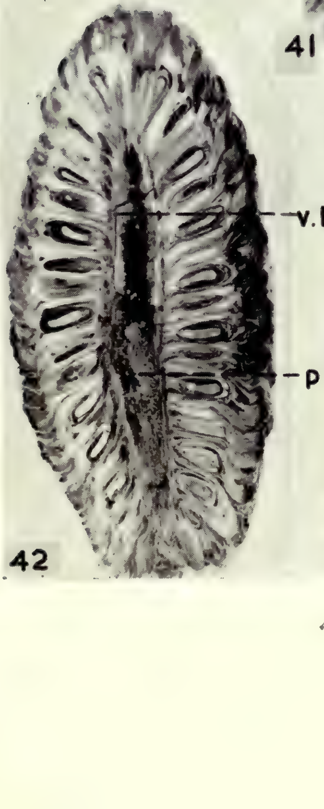

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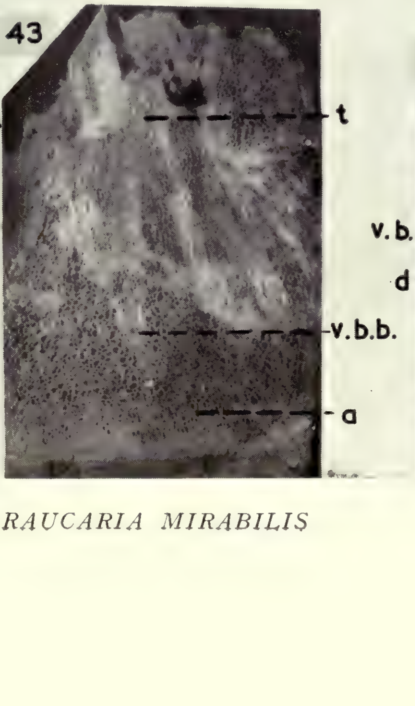

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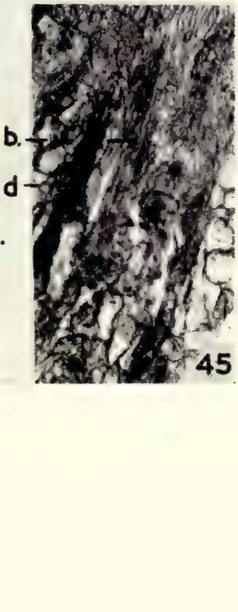

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*ARAUCARIA MIRABILIS*

## PLATE 5

*Araucaria mirabilis* (Spegazzini).

FIG. 46. Surface view of mature seed cone whose structure is illustrated in figs. 47–53. *l* = ligule, *a* = apophysis of bract. V. 30958. × 4·1.

FIG. 47. Detail of tangential longitudinal section of cone-scale from fig. 50; T.S. = testa of seed (stony layer), F = surface tissue of fertile scale, *en* = endosperm, E = embryo. V. 30958*a*. × 13.

FIG. 48. Detail of embryo seen obliquely cut in transverse section of cone in fig. 51 (E); *co* = cotyledon, *en* = endosperm. V. 30958*b*. × 25.

FIG. 49. Transverse section of embryo from tangential longitudinal section of cone (cf. fig. 47), showing two cotyledons (*co*). V. 30958*a*. × 25.

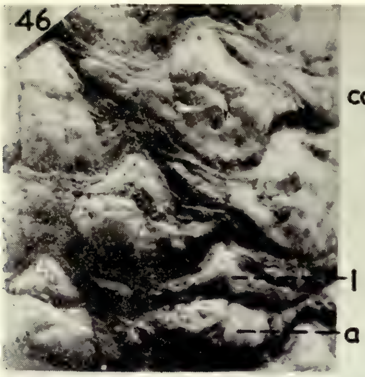
FIG. 50. Tangential longitudinal section of cone, showing cone-scales with seeds. *c* = cone-scale with wing, *S* = seed with endosperm and embryo, F = surface tissue of fertile scale. V. 30958*a*. × 4·1.

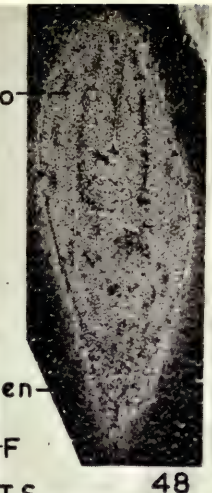
FIG. 51. Transverse section of cone; T.S. = testa of seed (stony layer), *en* = endosperm, E = embryo, *ss* = suspensors. V. 3098*b*. × 4·1.

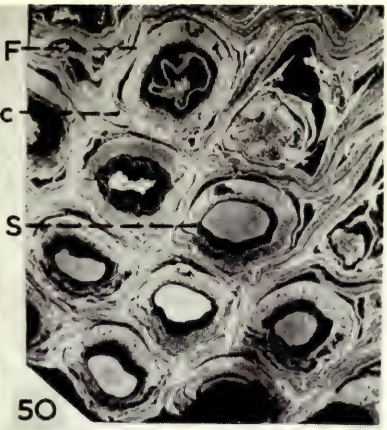
FIG. 52. Radial longitudinal section of cone; lettering as in fig. 51. V. 30958*c*. × 4·1.

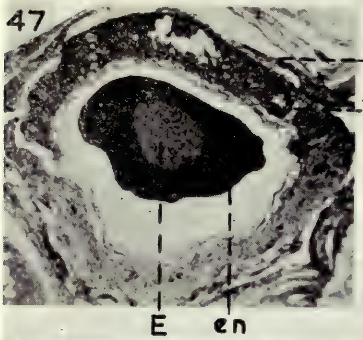
FIG. 53. Tangential longitudinal section of cone, taken at 1 mm. from outer surface; *l* = ligule with vascular bundles, *b* = bract with vascular bundles. V. 30958*d*. × 8.

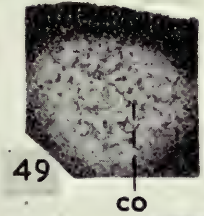
FIG. 54. Tangential longitudinal section of cone illustrated in Pl. 4, taken at level of ligule (*l*) and showing vascular bundles of ligule (*v.b.l.*), and vascular bundles of bract (*v.b.b.*) with ? resin ducts (*d*). V. 30957*a*. × 8.

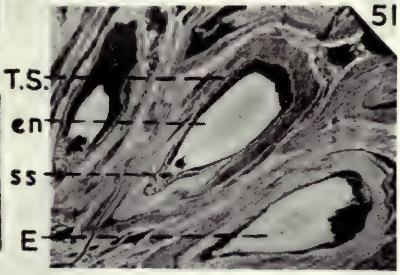


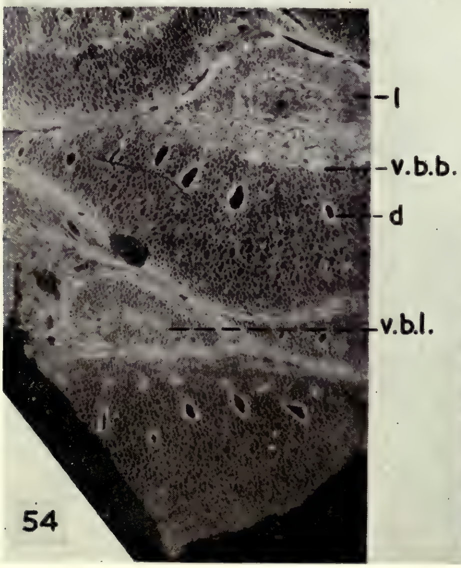











l
v.b.b.
d
v.b.l.
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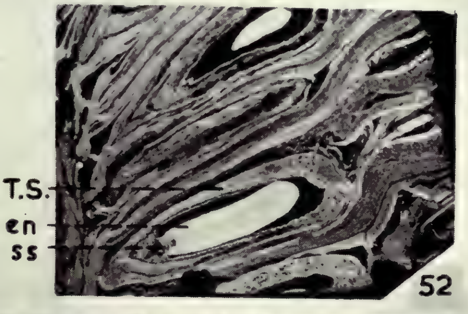
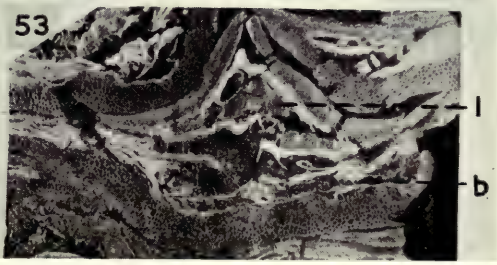




*ARAUCARIA MIRABILIS*

## PLATE 6

*Pararaucaria patagonica* Wieland.

FIG. 55. Cone showing fertile scales (*f*) and bracts (*b*), the surface features weathered. V. 30959. × 1.

FIG. 56. Cone showing less marked degree of weathering. V. 30960. × 1.

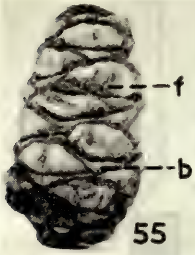
FIGS. 57–60. Tangential longitudinal sections (cf. also Text-fig. 6) through fertile scales and bracts, taken from base outwards. *f* = fertile scale, *f.s.* = vascular supply of fertile scale, *f.s.l.* = lateral bundle supplying seed in region of basal foramen, *sc* = sclerenchyma of fertile scale, *b* = bract, *b.s.* = vascular supply of bract, T.T. = transfusion tissue, *w* = wing tissue of testa of seed (cf. fig. 61), *t.s.* = stony layer of testa of seed, F = basal foramen of seed, E.*r.* = radicle of embryo, E.*c.* = cotyledons of embryo, *n* = nucellus, *e.s.* = embryo sac. Figs. 57–59, V. 30961*a–c*. Fig. 60, V. 30960*a* × 8.

FIG. 61. Stellate sclerotic tissue of wing of seed (cf. fig. 59, *w*). *t.s.* = stony layer of testa of seed. V. 30961*c*. × 50.

FIG. 62. Cone with surface features much weathered, showing foliated pedicel (*pl.*). V. 30962. × 1.

FIG. 63. Cone showing surface features of fertile scales and bracts, the fertile scales with vertical grooving of protruding abaxial surface. V. 30963. × 0·8.

FIG. 64. Detail of leaves on pedicel from cone in fig. 62, showing longitudinally striated abaxial surface. V. 30962. × 3·3.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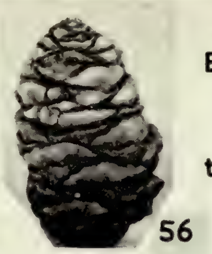
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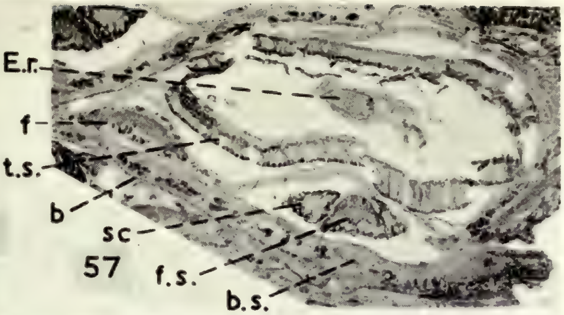
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E.r.
f
t.s.
b
sc
f.s.
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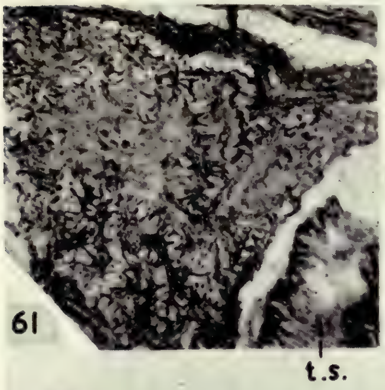
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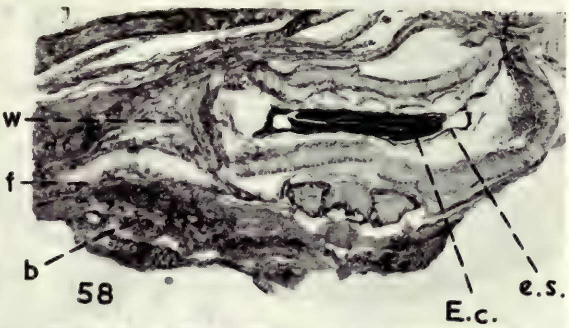
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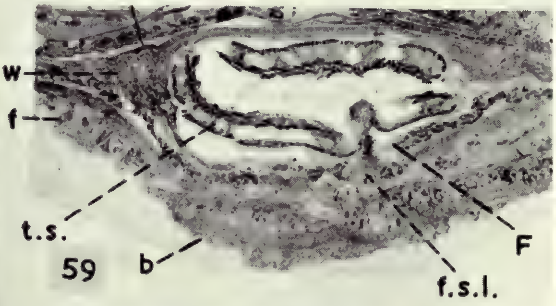
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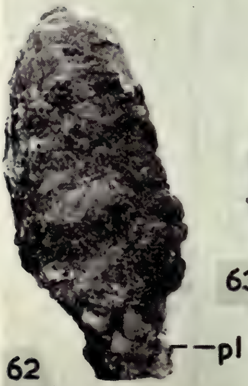
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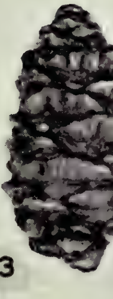
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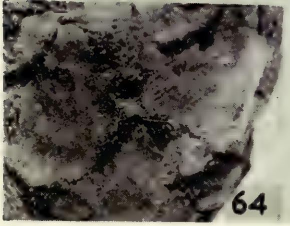
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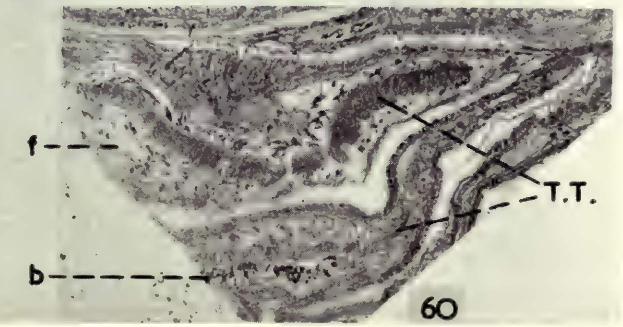
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*PARARAUCARIA PATAGONICA*

## PLATE 7

*Pararaucaria patagonica* Wieland.

FIG. 65. Transverse section of stele of cone axis in lower half of cone, showing narrow pith (*p*) and thick cylinder of xylem (*x*), with bract trace at *b*. V. 30964*d*. × 11·7.

FIGS. 66–72 illustrate structure of xylem of cone axis. V. 30959*d*.

FIG. 66. Radial longitudinal section of transitional region of xylem, showing from right to left the sequence from protoxylem (*px*) through metaxylem (*mx*) to secondary xylem. × 166.

FIG. 67. Detail of pitting in primary xylem from fig. 66, showing spiral pitted tracheids (*s.p.*) and reticulate tracheids (*ret.*). × 417.

FIG. 68. Radial longitudinal section of xylem showing, on the right, reticulate tracheids of primary xylem, and on the left, the radial walls of secondary tracheids (*sec.*) with uniseriate bordered pits. *m.r.* = medullary ray, × 166.

FIG. 69. Detail from fig. 68, showing pits on radial walls of secondary xylem tracheids, and part of medullary ray (*m.r.*) with cross-field pitting. × 333.

FIG. 70. Radial longitudinal section of secondary xylem at base of cone axis, showing uniseriate and biseriate (*bi*) radial pitting of tracheids, and medullary ray with cross-field pitting (*m.r.*) × 166.

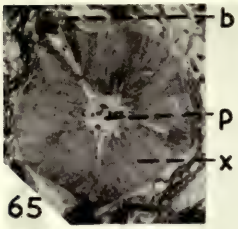
FIG. 71. Detail of biseriate pitting on radial walls of secondary tracheids, from fig. 70. × 333.

FIG. 72. Radial longitudinal section of secondary xylem in region of medullary ray, showing cupressoid cross-field pitting (*c*). (Longitudinal axis of cone runs across the photo.) × 417.

FIG. 73. Radial longitudinal section of fertile scale with seed and embryo, seen (reversed) at E in fig. 75, showing orientation of embryo. *c* = cotyledons, *r* = tip of radicle, *m* = closed micropyle. V. 30965*a* × 8.

FIG. 74. External features of long cone, showing weathered surfaces of fertile scales (*f*) and bracts (*b*). V. 30965. × 1·5.

FIG. 75. Median longitudinally cut surface of cone in fig. 74, showing fertile scales bearing seeds with embryos (E). *s* = axis stele. × 1·5.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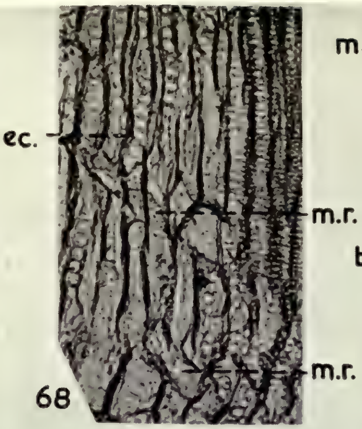
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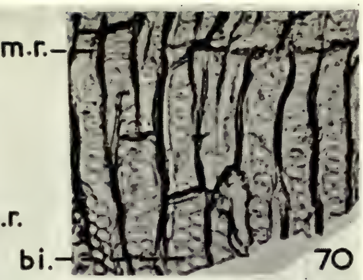
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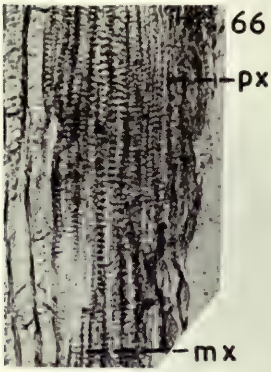
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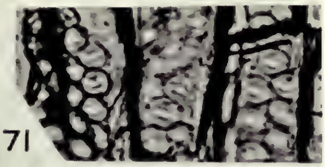
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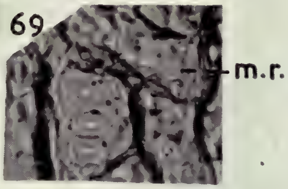
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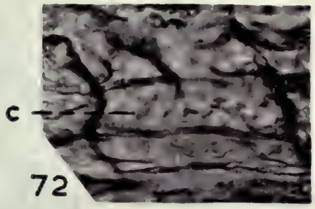
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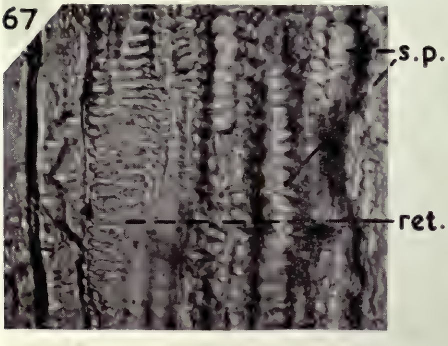
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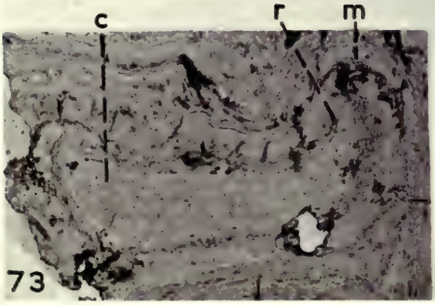
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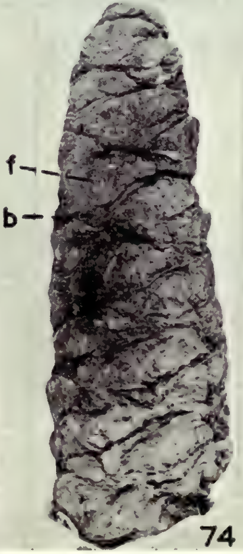
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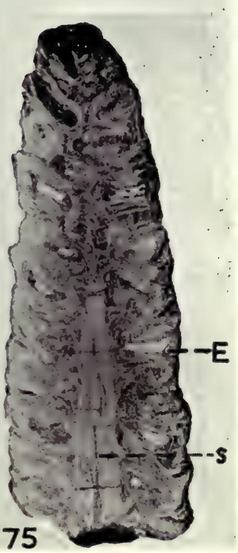
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# THE SOLUTION OF THE PILTDOWN PROBLEM

J. S. WEINER, K. P. OAKLEY

AND

W. E. LE GROS CLARK

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
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LONDON: 1953

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# THE SOLUTION OF THE PILTDOWN PROBLEM

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*Pp.* 139–146 ; *Pls.* 8, 9

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LONDON: 1953

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# THE SOLUTION OF THE PILTDOWN PROBLEM

*By* J. S. WEINER, K. P. OAKLEY & W. E. LE GROS CLARK

NOTE.—The curator of a palaeontological collection, which may contain rare specimens of great scientific importance, is frequently faced with the problem of whether to allow such specimens to be reinvestigated by treatment with acids, sectioning, removal of fragments for chemical analysis, or other methods which might seem to involve damage to a unique object. The cautious attitude of a previous generation has undoubtedly preserved for their successors many fossils which, for example, might have been damaged by mechanical treatment in the past, but can now be developed in perfection by more recently devised chemical methods. In the case of the Piltdown relics, one can be certain that after they came into the late Sir Arthur Smith Woodward's possession they would not have been treated or tampered with either chemically or physically. The decision to submit these specimens to a rigorous re-examination was made some years ago; the final result, unexpected at the time, will be found in the following pages.

W. N. EDWARDS, *Keeper of Geology.*

SINCE the report, some forty years ago,[1] of the discovery of several cranial fragments, a portion of a mandible and a canine tooth at Piltdown in Sussex, the problem of the "Piltdown skull" has been the subject of continuous controversy. Some authorities have accepted all the remains as those of an extinct type of hominid. But it is probably true to say that most anthropologists have remained sceptical or frankly puzzled by the contradictions which they present, for (apart altogether from other details) the combination of a cranium closely similar to that of *Homo sapiens* with a mandible and canine tooth of simian form seemed too incongruous. It has been suggested, indeed, that they really represent the fortuitous association of a Pleistocene human cranium with the remains of a fossil ape which had perhaps been secondarily derived from an earlier geological deposit. The application of the fluorine test (Oakley & Hoskins, 1950), however, made it quite clear that the mandible and canine were certainly not older than the cranium and, *on the assumption that they were all genuine fossils*, it naturally appeared to lend some support to those who held them to be contemporaneous and to belong to the same individual. It is also a fact that the remarkably flat wear of the molar teeth in the mandibular fragment is quite unlike that normally found in apes at a corresponding stage of dental attrition (though similar to the type of wear characteristic of the hominid dentition), while the mode of wear of the large canine tooth is also different from that which occurs in apes. But there is another possible explanation of the apparent contradictions shown by the Piltdown remains: that the mandible and canine tooth are actually those of a modern ape (chimpanzee or orang) which have been deliberately faked to simulate fossil specimens. It was not till one of us (J. S. W.) in the course of personal discussions put forward this proposition fairly and squarely as the only possible solution of the Piltdown puzzle, pointed out that the organic content of the mandible had never been examined, and moreover demonstrated experimentally that artificial abrasion of the teeth of a chimpanzee combined with appropriate staining produced an appearance astonishingly similar to the Piltdown molars and canine, that we decided on a critical re-study of all the Piltdown material with this specific possibility directly in view. The results of our investigations have now demonstrated quite clearly that the mandible and canine are indeed deliberate fakes. The evidence[1] for this conclusion is briefly as follows :

---

[1] Dawson & Woodward, 1913.

## EVIDENCE OF THE ARTIFICIAL ABRASION OF THE PILTDOWN TEETH

### *Molar Teeth of the Mandible*

(1) The occlusal surfaces (particularly of $M_2$) are planed down over almost their whole extent to a flatness which is much more even than that normally produced by natural wear (Pl. 9, fig. 2).

(2) The borders of the flat occlusal surfaces—particularly the lateral borders—are sharp-cut and show no evidence of the bevelling which is usually produced by natural wear (Pl. 9, fig. 1).

(3) The centre of the talonid basin in $M_2$ is unworn, and is bounded by a sharp-cut and unbevelled border of the planed surface of the crown. This appearance would be produced by artificial abrasion but would not be expected in natural wear (Pl. 9, fig. 1).

(4) The surface of the areas of dentine exposed on the antero-medial cusps of the two molars is quite flat and flush with the surrounding enamel, instead of forming a depression as would be expected in natural wear.

(5) In both molars much more dentine has been exposed on the antero-internal than the antero-external cusps. But in the course of natural attrition the lateral cusps of lower molar teeth are normally worn down more rapidly (and thus usually show a greater exposure of dentine) than the medial cusps (Pl. 9, fig. 1).

(6) The degree of wear in the two molars, $M_1$ and $M_2$, is almost identical. But in early stages of natural attrition $M_1$ is commonly (though not always) more severely worn than $M_2$ (Pl. 9, fig. 3).

(7) The planes of the flat occlusal surfaces of the two molars are not congruous, i.e., they do not fit together to form a uniform contour. Unless the teeth have been displaced from their natural position after death (for which there is no evidence), this incongruity is difficult to explain by natural wear (Pl. 8; 9, fig. 3).

(8) Inspection of the isolated molar tooth (referred to the specimen called Piltdown II) with a binocular microscope shows that the occlusal surface of the enamel has been finely scratched, as though by an abrasive.

### *Canine Tooth*

(1) The mode of wear of this tooth is unlike that found normally either in ape or human canines, for the abraded surface has exposed the dentine over the entire lingual surface from medial to distal border and at one point actually reaches the apex of the pulp cavity (Pl. 9, fig. 5).

(2) The condition of the apex of the root, and the wide and open pulp cavity seen in an X-ray photograph, indicate fairly certainly that the canine was still incompletely erupted or had only just recently completed its eruption. But this would be incompatible with the severe attrition of the crown if the latter were naturally produced (Pl. 9, fig. 4).

---

[1] The full evidence will be discussed in detail in a later number of this Bulletin.

(3) X-ray examination shows no evidence of the deposition of secondary dentine (with a constriction of the pulp cavity) which might be expected if the severe abrasion of the lingual surface of the crown were the result of natural attrition (Pl. 9, fig. 4).

(4) The abraded surface of the crown shows fine vertically disposed scratches (as seen under a binocular microscope) which suggest the application of an abrasive (Pl. 9, fig. 5).

## EVIDENCE OF THE FLUORINE CONTENT

The fluorine method as applied in 1949 (and reported in full in 1950) served well enough to establish that neither the Piltdown cranium nor the mandible was Lower Pleistocene. It did not distinguish (nor at that time was it intended to distinguish) Upper Pleistocene from later material. The rate of fluorination at this site has probably not been high enough to give a clear separation between Upper Pleistocene and, say, Early Post-glacial bones. Moreover the method of analysis used in 1949 was accurate only within rather wide limits when applied to samples weighing less than 10 milligrams, with the consequence that even the difference between the fluorine contents of fossil and modern specimens was obscured where the samples were of that order of magnitude. Improvements in technique have since led to greater accuracy in estimating small amounts of fluorine, and it therefore seemed worth while submitting further samples of the critical Piltdown specimens for analysis in the Government Laboratory. The new estimations, based mainly on larger samples, were made by Mr. C. F. M. Fryd. The following summary of the results leaves no doubt that, whereas the Piltdown cranium may well be Upper Pleistocene as claimed in 1950, the mandible, canine tooth and isolated molar are quite modern.

| | $\%F$ | $\frac{\%F}{\%P_2O_5} \times 100$ |
|---|---|---|
| Minimum F-content of local U. Pleistocene bones | 0·1 | 0·4 |
| *Ditto.* Upper Pleistocene teeth[1] | 0·1 | 0·4 |
| Piltdown cranium I | 0·1 | 0·8 |
| Piltdown cranium II: frontal | 0·1 | 0·8 |
| Piltdown cranium II: occipital | 0·03 | 0·2 |
| Piltdown mandible (bone) | <0·03 | <0·2 |
| Molar of Piltdown mandible | <0·04 | <0·2 |
| Piltdown canine | <0·03 | <0·2 |
| Isolated molar (Piltdown II) | <0·01 | <0·1 |
| Molar of Recent chimpanzee | <0·06 | <0·3 |

[1] All the tooth samples were *dentine*.

## EVIDENCE OF THE ORGANIC CONTENT

To regard the organic content of bones and teeth as a measure of their antiquity has long been regarded as fallacious, and for that reason no serious attempt has ever been made to test the relative ages of the various Piltdown specimens by that means. However, extensive chemical studies of bones from early occupation sites in North America by Cook & Heizer (1947) have shown that in bones preserved under broadly the same conditions the nitrogen of their protein (ossein) is lost at a relatively slow, and on an average almost uniformly declining, rate. Thus, N-analysis, used with discretion, can be an important supplement to F-analysis, and also for the relative dating of specimens too recent to be within the range of the fluorine method.

Dr. J. D. H. Wiseman and Mrs. A. Foster in the Department of Minerals of the British Museum have devised a method of estimating very small quantities of nitrogen, and Mrs. Foster, using this new method, determined the nitrogen content of a series of samples of the Piltdown material and of selected controls. The following is a summary of the results of this work which agree with all the other evidence indicating that the Piltdown mandible, canine and isolated molar (II) are modern. (The possibility that the Piltdown specimens were steeped in a gelatinous preservative has been borne in mind; if this had been the explanation of their nitrogen-content, the cranial bones which are porous would have shown *more* nitrogen than the highly compact dentine of the teeth; whereas the reverse is true.)

*Nitrogen-content of Bone Samples*

| | %*N* |
|---|---|
| Fresh bone | 4·1 |
| Piltdown mandible | 3·9 |
| Neolithic bone (Kent) | 1·9 |
| Piltdown I cranial bones (*average*) | 1·4 |
| Piltdown II frontal | 1·1 |
| Piltdown II occipital | 0·6 |
| U. Pleistocene bone (London) | 0·7 |

*Nitrogen-content of Dentine Samples*

| | %*N* |
|---|---|
| Chimpanzee molar | 3·2 |
| Piltdown canine | 5·1 |
| Piltdown I molar | 4·3 |
| Piltdown II molar | 4·2 |
| U. Pleistocene equine molar (Piltdown) | 1·2 |
| U. Pleistocene human molar (Surrey) | 0·3 |

## EVIDENCE OF THE COLOURING OF THE PILTDOWN SPECIMENS

A black coating—ferruginous according to Dawson & Woodward (1914: 87)—covers most of the surface of the Piltdown canine. When this tooth and the molars were sampled in 1948, one of us (K. P. O.) noted that " below an extremely thin ferruginous surface stain the dentine was pure white, apparently no more altered than the dentine of Recent teeth from the soil." Examination by Dr. G. F. Claringbull in the Department of Minerals has now shown that the coating on the canine is in fact non-metallic, it is a tough, flexible paint-like substance, insoluble in the common organic solvents, and with only a small ash-content. The extreme whiteness of the dentine and the nature of the black skin are thus both consistent with the evidence presented above for the essential modernity of the canine.

The mandible is of a reddish-brown colour which, though rather patchy, matches closely enough that of the cranial fragments to raise no suspicion that all the remains (from the original Piltdown site) might not belong to one skull. The frontal fragment stated to have been found at a second site (Piltdown II) is also of a similar brown colour but differs noticeably from the darker greyish-brown occipital fragment from the same site. That the colour of all these fragments is due to iron oxides has been confirmed by direct analysis in the Government Laboratory.

But whereas the cranial fragments are all deeply stained (up to 8% of iron) throughout their thickness, the iron staining of the mandible is quite superficial. A small surface sample analysed in 1949 contained 7% iron, but, when in the course of our re-examination this bone was drilled more deeply, the sample obtained was lighter in colour and contained only 2–3% of iron. The difference in iron staining is thus also in keeping with the other evidence that the jaw and the cranium are not naturally associated.

Smith Woodward recorded (1948: 59; see also 1935: 134) that " the colour of the pieces which were first discovered was altered a little by Mr. Dawson when he dipped them in a solution of bichromate of potash in the mistaken idea that this would harden them." Direct chemical analysis carried out by Drs. M. H. Hey and A. A. Moss in the Department of Minerals at the British Museum (Natural History), as well as the X-ray spectrographic method of Mr. E. T. Hall in the Clarendon Laboratory, Oxford University, confirmed that all the cranial fragments seen by Smith Woodward in the spring of 1912 (before he commenced systematic excavations) do contain chromate ; on the other hand, there is no chromate in the cranial fragments subsequently collected that summer—either in the right parietal, or in the small occipital fragment found *in situ* by Smith Woodward himself. This being so, it is not to be expected that the mandible (which was excavated later and in the presence of Smith Woodward, 1948: 11) would be chromate stained. In fact, as shown by direct chemical analysis carried out in the Department of Minerals of the British Museum, the jaw does contain chromate. It is clear from Smith Woodward's statement about the staining of the cranial fragments of Piltdown I (which we have verified), that a chromate staining of the jaw could hardly have been carried out without his knowledge *after* excavation. The iron and chromate staining of the Piltdown jaw seems to us to be explicable only as a necessary part of the deliberate matching of the jaw of a modern ape with the mineralized cranial fragments.

This grave interpretation, which we have found difficult to avoid, receives support from the finding that the frontal and occipital fragments labelled Piltdown II (and found three years later) contain small amounts of chromate. The piece of frontal bone, anatomically, could form part of the cranium of Piltdown I, and in colour and in its content of nitrogen and flourine it resembles the first occipital of Piltdown I rather than that of Piltdown II. Just as the isolated molar almost certainly comes from the Piltdown mandible, it seems only too likely that this frontal fragment originally belonged to the cranium of Piltdown I.

From the evidence which we have obtained, it is now clear that the distinguished palaeontologists and archaeologists who took part in the excavations at Piltdown were the victims of a most elaborate and carefully prepared hoax. Let it be said, however, in exoneration of those who have assumed the Piltdown fragments to belong to a single individual, or who, having examined the original specimens, either regarded the mandible and canine as those of a fossil ape or else assumed (tacitly or explicitly) that the problem was not capable of solution on the available evidence, that the faking of the mandible and canine is so extraordinarily skilful, and the perpetration of the hoax appears to have been so entirely unscrupulous and inexplicable, as to find no parallel in the history of palaeontological discovery.

Lastly, it may be pointed out that the elimination of the Piltdown jaw and teeth from any further consideration clarifies very considerably the problem of human evolution. For it has to be realized that " Piltdown Man " (*Eoanthropus*) was actually a most awkward and perplexing element in the fossil record of the Hominidae, being entirely out of conformity both in its strange mixture of morphological characters and its time sequence with all the palaeontological evidence of human evolution available from other parts of the world.

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## EXPLANATION OF PLATES

### PLATE 8

Fig. 1. The Piltdown mandible. Natural size. (1) Outer view; (2) inner view.

[*Photographs by C. Horton.*]

### PLATE 9

Fig. 1. The second molar tooth of the Piltdown mandible viewed from its occlusal aspect. × 4 diam. approx. Note the relatively large area of dentine exposed on the antero-internal cusp, and the sharp margin separating the central depression (talonid basin) of the tooth from the completely flattened cusps. Note also the sharp external margin of the " occlusal " surface, with no bevelling.

Fig. 2. The second molar tooth of the Piltdown mandible, viewed from the medial aspect. × 4 diam. approx. Note the extreme evenness of the flat " occlusal " surface.

Fig. 3. The first and second molar teeth of the Piltdown mandible viewed from behind. × 4 diam. approx. Note that the " occlusal " planes of the two teeth are set at an angle to each other.

Fig. 4. Radiograph of the Piltdown canine taken in an approximately antero-posterior plane. × 2 diam. approx. Note the thinness of the dentine on the lingual surface towards the apex of the tooth. At one point here the pulp cavity appears to have been exposed and the opening plugged with some material containing radio-opaque particles. The pulp cavity has been packed from the other end with mineral grains.

Fig. 5. The Piltdown canine tooth viewed from the lingual aspect. × 4 diam. approx. Note the fine scratches disposed mainly in a vertical direction. A little above the middle of the surface, towards the apex of the tooth, is seen a small oval area of lighter shade, marking the point where the pulp cavity has been opened by abrasion.

Fig. 6*a–c*. Samples of bone, drilled by L. E. Parsons using a parallel burr size 6, from: (*a*) Piltdown mandible; (*b*) mandible of Recent chimpanzee; (*c*) Piltdown skull (right parietal). × 15. Note that *a* and *b* consist of minute shavings, whereas *c* is a powder.

[*Photographs: C. Horton; X-ray of Fig. 4 by P. E. Purves.*]

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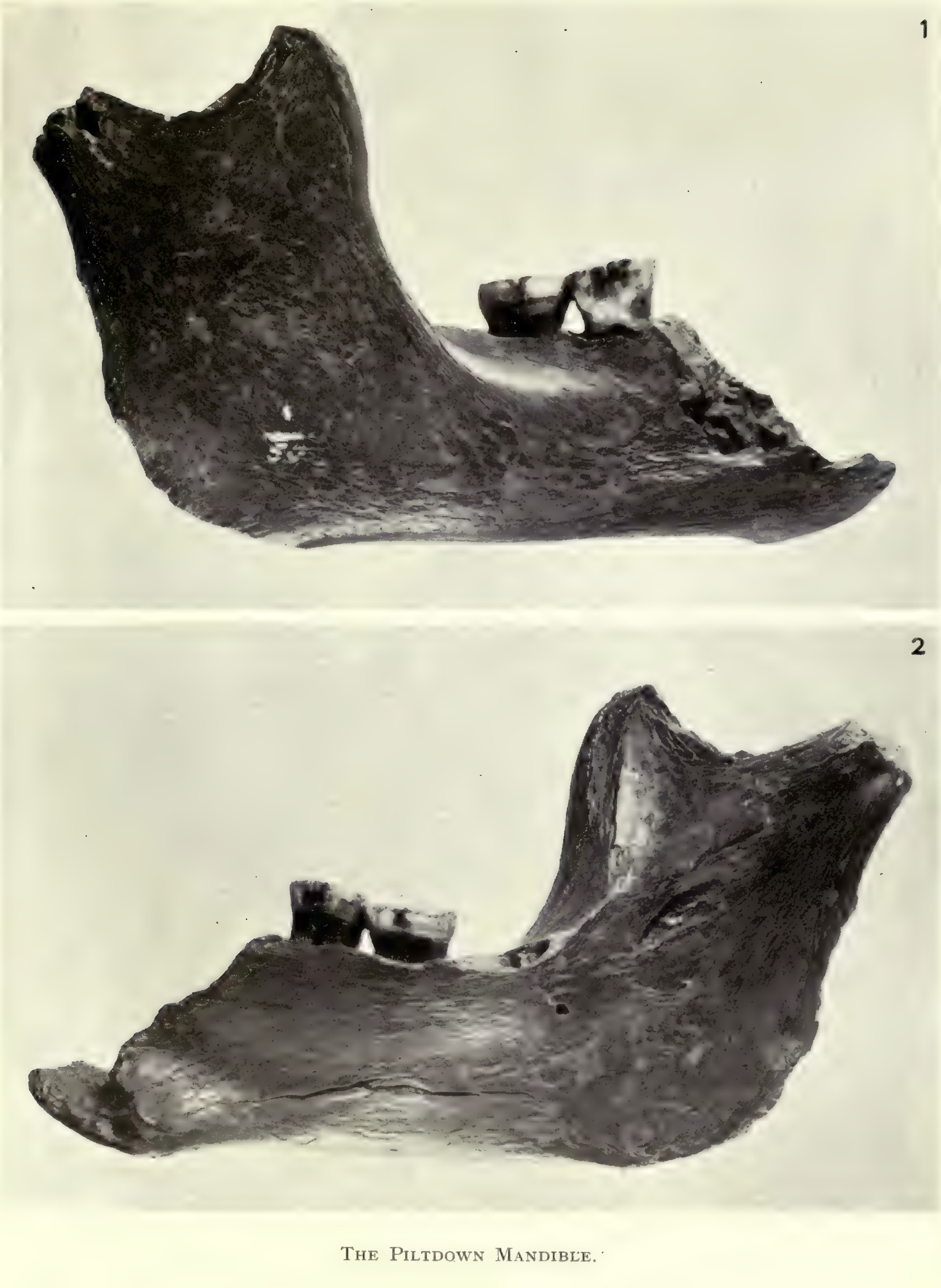
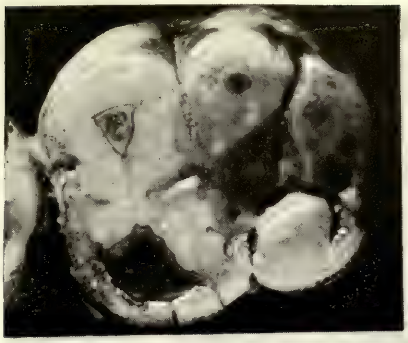


THE PILTDOWN MANDIBLE.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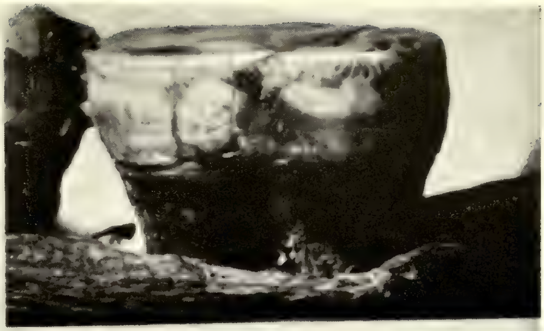
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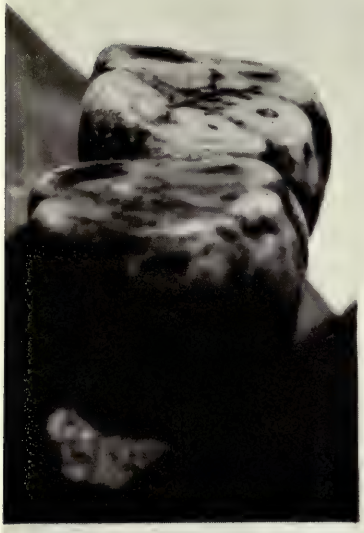
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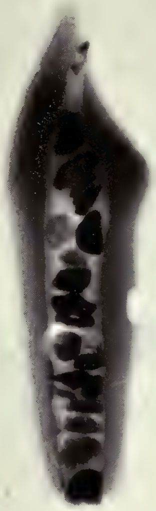
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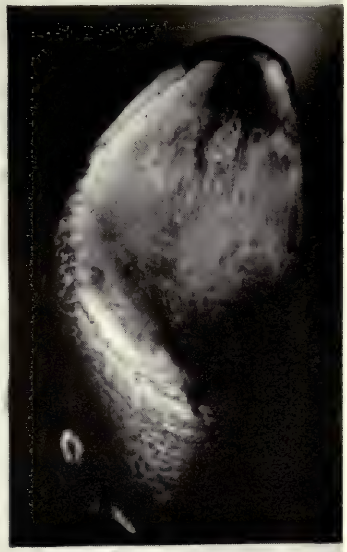
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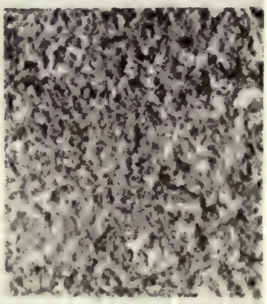
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Piltdown Teeth and Bone.

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M. E. J. CHANDLER

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# SOME UPPER CRETACEOUS AND EOCENE FRUITS FROM EGYPT

BY

MARJORIE E. J. CHANDLER

(With Appendices by M. Y. HASSÁN and M. I. YOUSSEF)

*Pp.* 147–187 ; *Pls.* 10–16 ; 1 *Text-figure*

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# SOME UPPER CRETACEOUS AND EOCENE FRUITS FROM EGYPT

*By* M. E. J. CHANDLER

## SYNOPSIS

The occurrence and preservation of fruits and seeds from the Dano-Montian and Eocene of Egypt is described, and previous work summarized and in some instances revised.

These Egyptian fossils are clearly related to the London Clay Eocene plants on the one hand and to the Recent flora of South-Eastern Asia on the other as shown by the occurrence of *Nipa* in all three floras. The historical and geographical connexion of the three floras is considered, due attention being paid to recent work on plant migration by Chaney and Axelrod. The conclusion is reached that whereas all Tethyan (Indo-Malayan) types of flora may have their remote origin in a uniform palaeotropical plant belt in Early or Middle Cretaceous times, some secondary centre of colonization must be postulated for the Eocene tropical flora of Western Europe where the original palaeotropical angiosperm flora must have been exterminated by the Cenomanian transgression.

The obvious source of recolonization lay in South-Eastern Asia, because the great East–West Tethyan ocean must have constituted a formidable barrier to mass migration from the African continent. Moreover the marked Malayan relationship of the London Clay flora supports its immediate Asiatic origin. Detailed systematic descriptions of the Egyptian fruits are given.

## INTRODUCTION

A few fossil fruits recently discovered in Egypt were sent to the British Museum for identification. They are of great importance, for hitherto the bulk of our knowledge of the ancient flora of North Africa has been derived from the study of wood (Kräusel, 1939), whereas fruits and seeds were almost unknown. The majority of the specimens came from the Dano-Montian Lower Esna Shales between latitudes 25° and 27° N. They were collected by two Egyptian geologists, Doctors M. Y. Hassan and M. I. Youssef, who in appendices to this paper give details of the deposits which yielded the fruits. (See also note on p. 187).

Dr. Hassan's finds were from the Kharga Oasis of the Western Desert, Dr. Youssef's from the Kosseir area bordering the Red Sea.

Like the London Clay, with which comparison will be made in the following pages, these plants occur in marine beds with a marine fauna, and must be presumed to have been derived from the nearby land surface of the African continent a little further south.

By a curious coincidence a fruit from the Lutetian (or possibly slightly younger beds of Eocene age) of Egypt was also received for study at about the same time. It was collected by members of the Anglo-Egyptian Oil Company, Messrs. Thiébaud and Robson, at Wadi Rayan in the Western Desert, i.e., at about latitude 29° N. in the Fayum. It is an extremely puzzling specimen, and some points about its anatomy are rather obscure.

The preservation of these fruits and seeds is interesting and somewhat variable. Some of them, e.g., *Palaeowetherellia*, are reproduced cell by cell in limonite in part at least. Indeed they display the details of their structure almost as well as the pyritized fruits of the London Clay. They have the merit of being more stable and permanent in their preservation than pyritized specimens, but this advantage carries with it the disadvantage that they do not so readily disintegrate and fall to pieces along structural lines and natural planes of weakness as the London Clay pyritized fossils so frequently do. Some of the best and most delicate evidence from the London Clay fruits came from decaying specimens, not from those which were artificially sectioned.

But some of the Egyptian fossils, e.g., Icacinaceae, have the appearance of being purely internal casts, for although they were already chipped, no cell-structure was exposed, or if visible was so indurated as to show little detail. Such specimens are unlikely to provide more information if broken or sectioned, and it therefore seems pointless to sacrifice them where clear and unmistakable evidence of internal structure along natural planes of weakness is lacking. It is highly probable that future collectors will in due course supplement the present meagre evidence from such tantalizing casts.

Several of the new Dano-Montian specimens agree with one (V.12985) which has been in the collection at the British Museum (Natural History) since 1912. This was described by Kräusel (1939 : 106, pl. 2, figs. 9, 10 ; text-fig. 32) and was referred by him to *Diospyros schweinfurthi* Heer. It came from the Lower Danian of Farafra in the Western Desert at latitude 27° N. approximately. Heer's supposed *Diospyros* and another specimen which he named *Royena desertorum* were originally described by him in 1876 (see p. 168).

The examination of the new material, and more especially of a newly fractured surface of V.12985, leaves no doubt that Heer's " *Diospyros* " and " *Royena* " both belong to a single species which has no connection with the Ebenaceae. The species, named hereafter *Palaeowetherellia schweinfurthi* (Heer), is obviously closely related to *Wetherellia variabilis* Bowerbank from the London Clay, and to another species *W. dixoni* (Carruthers)—to be redescribed—from the Bracklesham Beds of Selsey. The genus is now referred tentatively to the family Euphorbiaceae.

Apart from the above, only six Tertiary angiosperm fruits from Egypt have previously been recorded :

*Palmacites rimosus* Heer from the Danian of Kharga (Heer, 1876 : 11, pl. 1, figs. 21, 22), an imperfect fruit of which no really distinctive characteristics are shown or described. The anastomosing " fibres " in fig. 22 may be nothing more than compression ridges such as are seen in places on the fruit of *Icacinicarya youssefi*. Heer's determination must be regarded as very doubtful pending re-examination of the specimen.

*Securidaca tertiaria* Engelhardt (1907 : 213, pl. 19, fig. 6) from the Eocene of the Fayum. It would be unwise to comment upon this aceriform fossil without the most careful scrutiny of the original material combined with a comprehensive study of living fruits of this type in the various families in which they occur.

*Nipadites sickenbergeri* Bonnet from the Middle Eocene Nummulitic Limestone

(Marine Lower Mokattam of Gebel Giuchi, Mokattam), a species which the available evidence identifies with *Nipa burtini* (Brongniart) (see pp. 159, 162).

*Rubiaceocarpum markgrafi* Kräusel from the same beds which is clearly the same *Nipa* represented by seeds with outer integument preserved (see pp. 161, 163).

*Nymphaeopsis bachmanni* Kräusel from the Lower Oligocene of Cairo (Kräusel, 1939 : 39, pl. 2, figs. 2–8 ; pl. 3, fig. 8 ; pl. 21, fig. 6 ; text-fig. 7) has features which suggest that puzzling material has been wrongly interpreted. Further reference is made to the matter on p. 183 when the structure of *Thiebaudia rayaniensis* is discussed.

*Teichosperma spadiciflorum* Renner (1907 : 217 ; Kräusel & Stromer, 1924 : 33, pl. 1, fig. 2 ; text-figs. 1–3) from the Lower Oligocene of the Fayum, referred tentatively by Renner and with more certainty by Kräusel & Stromer to Pandanaceae, needs re-investigation especially as regards the number of locules and form of the seed. If the seed is really curved as Kräusel & Stromer's text-fig. 3 shows, the family Myrtaceae should be explored. But before making confident statements about this, it might be necessary to examine serial sections. Without further evidence no really satisfactory determination can be made, although relationship to Pandanaceae seems highly improbable.

It is not surprising that fruits from a remoter period of angiosperm history than the Tertiary material hitherto studied are difficult to relate to living genera or to place in Recent plant families. But in spite of the fact that it has not been possible to identify all the specimens, the interest and significance of this tiny flora are out of all proportion to its size.

The list of the newly found plants is given below.

| | | Horizon and locality | | |
|---|---|---|---|---|
| Family | Genus and species | Lower Danian | Dano-Montian | Lutetian (approx.) |
| Nipaceae | *Nipa burtini* (Brongn.) | — | Kosseir | — |
| Anonaceae | *Anonaspermum aegypticum* n. sp. | — | ,, | — |
| Euphorbiaceae | *Lagenoidea trilocularis* Reid & Chandler | — | ,, | — |
| | *Lagenoidea bilocularis* Reid & Chandler | — | ,, | — |
| Euphorbiaceae ? | *Palaeowetherellia schweinfurthi* (Heer) | Farafra | Kharga and Kosseir | — |
| Icacinaceae | *Icacinicarya youssefi* n. sp. | — | Kosseir | — |
| | *Icacinicarya* sp. ? | — | ,, | — |
| Flacourtiaceae ? | *Thiebaudia rayaniensis* n. gen. et sp. | — | — | Wadi Rayan |
| *Incertae sedis* | *Carpolithus hassani* n. sp. | — | Kharga | — |
| | *Carpolithus* sp. (*Icacinicarya* ?) | — | ,, | — |
| | *Carpolithus* sp. | — | Kosseir | — |

Fuller details of localities are given under the descriptions of the species in the systematic part of this paper. No attempt has been made to determine a few small twigs.

These discoveries are of outstanding importance for a number of reasons :

(1) As stated above, fossil fruits and seeds of any age are rare in Egypt. The recent finds suggest that careful collecting, persisted in over a long period, would reveal the presence of a considerable flora in that region.

(2) Very little is known about pre-Tertiary angiosperm fruits and seeds from any area whatsoever. Knowledge derived from leaves or wood is usually complementary to that based on fruits and seeds rather than strictly comparable with it. This was discussed by Reid & Chandler (1926 : 10–13). Plant organs such as leaves tend to be preserved in different deposits from fruits and seeds and to represent different elements in the parent plant-formations. But here in Egypt are data from pre-Tertiary Beds which are really comparable with the abundant Tertiary records of fruiting organs elsewhere.

(3) The plants from Egypt are quite obviously related to the Tethyan type of flora found in the London Clay. For even in so small a group as this under discussion similar or identical genera and even species occur. Note the presence of *Palaeowetherellia* (a distinct genus and species representing *Wetherellia*), of a *Nipa*, of the two species of *Lagenoidea* actually found in the London Clay (so far as present information can demonstrate), of an *Anonaspermum*, and of the family Icacinaceae. Here is impressive evidence that the Malayan type of flora so characteristic of the London Clay was already present in Africa towards the end of Cretaceous times. It must be presumed to have flourished on the southern sea-board of the ancient Tethys ocean.

(4) The presence in Egypt of a flora of strong tropical Malayan affinity, for such must be the relationship of any flora at all comparable with that of the London Clay, confirms the view supported by other lines of evidence that the climate of Africa to the north of the equatorial belt must have been remarkably different during the late Cretaceous and Eocene from what it is today. *Nipa* and its associates demand not only warmth but a high degree of humidity (Reid & Chandler, 1933 : 74 *et seq.*).

The discovery of this Tethyan flora in Egypt at the end of the Cretaceous must inevitably raise the question, " What was its historical and geographical connection with the biologically similar floras in the London Clay in Eocene times and in Indo-Malaya at the present day?"

Did the Egyptian flora with the characteristic *Nipa* and its associates arise in remote times in South-East Asia and spread thence into the African and European continents as climatic conditions, combined with available migration routes, favoured its expansion, or had it some other origin ? From what primitive source or sources were these three related floras derived ?

Professor Kryshtofovich expressed the opinion that in the tropics of South-East Asia the Malayan type of flora had remained " unmolested ever since its first descent from its Cretaceous ancestors " (1929 : 310, 311).

Reid & Chandler (1933 : 82) stated that in their opinion the London Clay flora had its origin in Malaya, whence it migrated northwards and westwards along the shores of the Tethys ocean to Western Europe.

The late Professor Seward criticized the views of these three authors on the grounds that the early Tertiary flora of South-East Asia is but little known, and that the evidence concerning it, if it exists at all, has not yet been published (1934 : 23), so that there may, for all we know, have been no Tethyan type of flora in Indo-Malaya in the early Tertiary which could have served as a centre of dispersal.

He propounded two alternative suggestions as to the origin of the Tethyan flora in Europe :

(1) That like the later Tertiary floras it may have reached Europe " not from a South-Eastern home but from the North."

(2) That the London Clay flora may have been part of a widespread flora " which in the course of the Tertiary period suffered progressive reduction and is now represented by enfeebled relicts in Indo-Malaya."

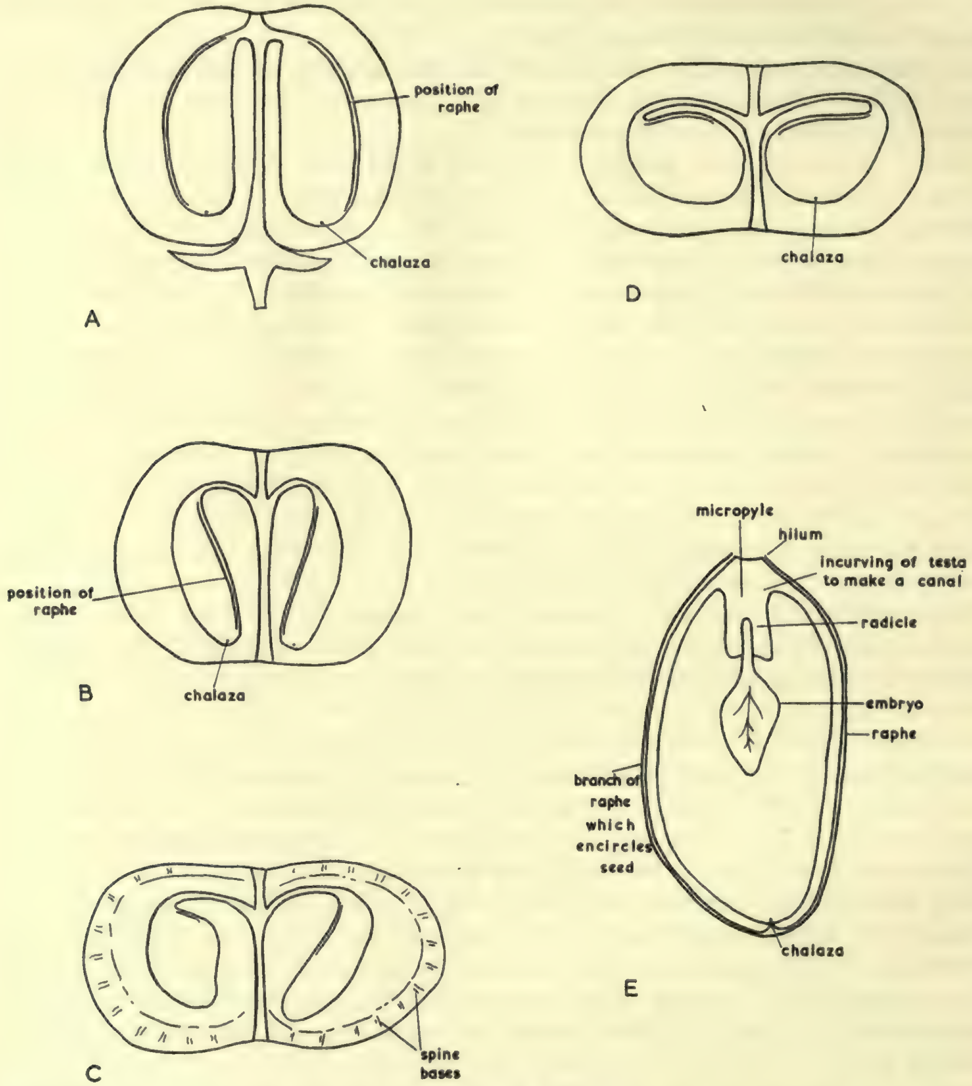
Before discussing these suggestions it may be of value to digress so as to take account of recent important American contributions to plant history set forth by Professor Chaney in two papers (1940, 1947). Chaney bases his views on successive American fossil floras. These show that there was gradual displacement of temperate to warm-temperate Cretaceous forests in low and middle latitudes in the United States at the end of the Cretaceous period. Their place was taken by warm temperate to sub-tropical vegetation (the Neotropical flora of Chaney) of Lower Eocene age derived largely from the Antillean region on the East, and from Mexico and Central America on the West. Evidently, he states, an early Tertiary *northward* movement of plant populations as a whole occurred, so that the temperate forest type of vegetation became concentrated in high latitudes, while tropical and sub-tropical vegetation, now characteristic of forests near the Equator, spread into middle latitudes, reaching 50° N. approximately on the western side of the continent, and 37° N. on the eastern side.

Professor Chaney compares American plant history with that of the Old World, and emphasizes that in approximately the same period a parallel story of plant migration occurs there, modified to some extent by the extensive East-West barrier of the Tethys ocean, which caused some differentiation of vegetation to the North and South of it in Eocene and later times. He makes special mention of the tropical Malayan London Clay flora at latitude 50° N. on the west side of the Eurasian continent whose modern equivalents (notably *Nipa* and mangrove) grow in the rain-forest of Indo-Malaya. He also lists and shows on a map (1940 : 482, 483, text-fig. 1) numerous Eocene and a few Oligocene (palaeotropical) floras of the Old World which have similar tropical relationship, while localities for the corresponding (neotropical) floras in the New World are also plotted. He then recalls that since the Oligocene a reverse movement has taken place in both hemispheres, the sub-tropical and tropical forests gradually moving south again, giving way both in North America and in Eurasia to that temperate vegetation which he calls the Arcto-Tertiary flora.

In America the tropical vegetation has survived in the Antilles, the North of South America, Central America and Mexico, with a few remains in South Florida. In Eurasia it survives in south-east Asia.

Chaney perceives that such a wide-spread shifting of forest distribution must be due to factors which were world-wide in operation, affecting whole plant populations

(1947 : 141). If, as appears from the evidence available, he is right that migration from the end of the Cretaceous onwards to the Oligocene was northwards, so that plants from equatorial regions extended into middle latitudes, then the suggestion made by Seward that the Eocene tropical floras, like the later ones, may have reached Europe from the North does not fit into the picture and cannot be seriously enter-


position of raphe
chalaza
A
chalaza
D
position of raphe
chalaza
B
micropyle
hilum
incurving of testa to make a canal
radicle
embryo
raphe
branch of raphe which encircles seed
chalaza
E
spine bases
C

TEXT-FIG. 1. A–D Longitudinal sections through fruits showing placentation (diagrammatic). A. *Diospyros* sp. Recent. B. *Wetherellia variabilis* Bowerbank. London Clay; Sheppey. C. *Wetherellia dixoni* (Carruthers). Cuisian ?; Selsey. D *Palaeowetherellia schweinfurthi* (Heer). Upper Cretaceous; Egypt. E. Longitudinal section through seed, *Diospyros* sp. Recent.

tained. There is certainly no evidence in Europe of a Malayan flora in more northerly stations than the London Basin.

Reid & Chandler (1933 : 62) were convinced by its past distribution and present physiological requirements that the *Nipa* flora in the London Clay was living at the most northerly limit of the climatic conditions (both of temperature and humidity) which it could tolerate. Hence it is improbable that it could have come into being in yet more northerly regions which would have been still more unfavourable in these respects, regions which were, moreover, already occupied by the Arcto-Tertiary type of vegetation suited to them. For these reasons the origin of the Malayan flora to the North appears to be untenable.

Before considering Seward's other alternative suggestion, it may be helpful to summarize briefly the facts (and deductions from them) which should be borne in mind and correlated in any further consideration of these problems. They are as follows :

(1) A late Cretaceous Tethyan flora in Egypt found at approximately 25° to 30° N. probably derived from the African mainland at no great distance to the South.

(2) An early Eocene Tethyan flora in Western Europe extending North to latitude 50° approximately.

(3) The presence of similar tropical or sub-tropical floras in the Eocene and Oligocene situated apparently along the former northern boundaries of the Tethys ocean, as many of these floras yield *Nipa*.

(4) A living Tethyan type of flora restricted to South-East Asia (the Indo-Malayan flora).

(5) A northward extension of the equatorial tropical forest belt between Cretaceous and Oligocene times coinciding with the broadened latitudinal belt of increased temperature and humidity.

With these facts and deductions in mind, we now turn to Seward's second alternative theory, viz., that the Tethyan flora was part of a widespread flora which suffered progressive reduction, surviving in Indo-Malaya today. This is an unquestionably true statement, for on actual fossil evidence, so far as it goes, the flora of Indo-Malaya, or something closely akin to it, was once much more widely distributed (Chaney, 1940 : 482–485, text-figs. 1, 2 ; Edwards, 1936 : 28, text-fig. 9, map showing the distribution of *Nipa* in relation to the approximate outlines of the Tethys ocean). But Seward's statement does not carry the matter far enough ; it requires much more elucidation. Nor does it exclude the possibility of an *immediate* (early Eocene and post-Cretaceous) Malayan origin for the palaeotropical vegetation of Europe.

In support of the theory that the various Tethyan floras originated within a uniform tropical belt of vegetation reference may be made to Axelrod (1952). He believes that in the Lower Cretaceous, "long distance migration may have been more effective than at any later time," producing a more or less uniform type of vegetation within given climatic belts.

During that period, he points out, the angiosperms were beginning to compete successfully with the older waning Mesozoic floras which they were in process of supplanting. He visualizes that by Middle Cretaceous times there must have been basic, more or less world-wide, angiosperm floras with the minimum of regional differentiation, viz., a tropical to sub-tropical flora in lower and middle latitudes more uniform in type throughout the world than has existed at any time since that period, and a uniform temperate flora at higher latitudes.

It is not unreasonable to suggest that Axelrod's uniform tropical angiosperm flora was the source from which the Recent tropical flora of South-East Asia and the Cretaceous-Oligocene tropical flora of North Africa were derived by direct and unbroken descent within these two regions. It may also have been the source of the Eocene European tropical flora, not by direct descent in Western Europe but by a more circuitous route. These suggestions are considered and explained in greater detail below.

There is no reason to think that in Equatorial Asia there was ever a period during the Tertiary when tropical conditions did not persist. Therefore it is not unreasonable to postulate that the old palaeotropical flora probably survived over the equatorial belt in that part of the world throughout Tertiary times, even after the Oligocene, when it was driven south of its maximum Eocene extension. In that equatorial belt it would have retained or gradually evolved a character of its own, viz., that of the Indo-Malayan flora as we know it today. This is essentially the opinion expressed by Kryshtofovich and quoted on p. 152.

In Africa the course of events may have been somewhat similar. Following upon the contraction of the Tethys sea in Oligocene and later times and the resulting climatic changes, the Tethyan flora must have been driven from the more northerly part of its former Cretaceous and Eocene territory by the pressure of unfavourable conditions. But it could probably have survived in the tropics of Central Africa. Desiccation combined with the southern trend of plant migration in post-Oligocene times would undoubtedly have prevented any later return to the more northerly latitudes it had previously occupied. Deserts and the Tethyan sea (or its shrunken remains) would probably have cut it off effectively from Asia. But within the African equatorial belt it may have persisted, possibly giving rise (or giving place ?) eventually to a distinctive African tropical vegetation as it evolved in isolation from the Asiatic stream of life.

But what of the London Clay Eocene flora of Britain, and how was it related to the uniform palaeotropical flora of Lower Cretaceous times ?

There can be no doubt that the Lower Cretaceous flora of this country must have been eliminated by the great marine transgression of the Upper Cretaceous. This transgression far overpassed the most northerly limits of tropical climate for which there is any evidence, viz., about latitude 50° N. If the European Lower Cretaceous palaeotropical flora persisted at all it must have been on islands, or on tracts of land on the western borders of the present European continent, perhaps on land margins now submerged beneath the sea. If Chaney is right about the world-wide character of climatic changes, the flora could not, in all probability, have survived unless land nearer the Equator was accessible for colonization during the late Cretaceous. For in America, as we have seen, temperate and warm-temperate forests occupied low and middle latitudes at this period, from which latitudes they were driven only at the end of the Cretaceous by the northward march of Equatorial vegetation. It seems obvious that with the withdrawal of the Upper Cretaceous sea the re-exposed land surface (now having a sub-tropical or tropical climate) would have been available for recolonization by a flora of tropical type. This may have come either from southern and western plant " reserves " as suggested above, or from the only two alternative sources, viz., the African continent, or the south-east of Asia. In the former we know that a Tethyan flora was present in the late Cretaceous. In the latter there is no reason to doubt the existence of such a flora at that time as has been pointed out above.

The theory of recolonization from the west offers no adequate explanation of the marked Indo-Malayan aspect of the incoming Eocene flora. It is unlikely that closely parallel development would have taken place independently in two such widely separated areas. It is equally improbable that the source of recolonization was the African continent. Had no serious physical barrier existed, the natural solution of the problem would be to assume that by Eocene times the Cretaceous Tethyan flora of Africa had migrated northwards and spread into Europe, as it followed the extension in latitude of the hot and humid climatic belt favourable to it.

But the existence of the great ocean barrier of the Tethys over perhaps 1,000 miles or more from South to North must have had a marked deterrent effect.

Axelrod (1952) discusses conditions affecting the migration of faunas and floras in geological times. He maintains that plant distribution at any particular time is " largely a reflection of the climates available for occupancy " (p. 177), i.e., climate is the chief factor controlling plant migration. But whereas he considers that a much higher degree of probability exists for plants than for animals in the matter of over-water dispersal, he is also sure that " within any given climatic region distance will finally impose a barrier to the migration of plants also." It is only fair to him to state that in spite of this, he regarded the presence of palaeotropical Tertiary vegetation on both sides of the Tethys as evidence that the sea in this particular case (as well as in others) did not prevent the distribution of the flora on both sides of it (1952 : 187). But this is a curious conclusion to have drawn, for he also explains that " The water barrier that a continental flora can transgress within an epoch of time (say, 10 to 15 million years) is not unlimited," while beyond 200 to 250 miles the probability of colonization by a whole flora is low. Hence what he designates the " waif assemblages " of ocean islands which lack balance, since whole classes and orders expected are absent, while others are only poorly represented. " It would appear," Axelrod writes, " that long-distance, over-water migration has not been generally effective in populating widely separated continents." Even during much longer periods of time, therefore, there may be good reason to doubt whether the Tethyan flora in Africa could have migrated directly across the great ocean which lay athwart its path to the North. Further, as Reid & Chandler (1933) pointed out, the London Clay flora shows far less affinity with the flora of Africa than with that of South-East Asia.

To the present writer, therefore, it seems highly improbable that wholesale migration took place across the Tethys.

There remains the third suggested source for the post-Cretaceous colonization of

West Europe, namely the South-East Asiatic. On such evidence as is available this appears to be by far the most probable source for these reasons :

(*a*) The Indo-Malayan region and Southern England both lay within the palaeotropical climatic belt of Eocene times.

(*b*) The northern shores of the Tethys and the land adjoining were so situated as to provide a possible migration route from South-East Asia to West Europe within this greatly extended tropical belt of Eocene times which allowed the flora of equatorial regions to occupy many degrees of latitude North of its present limits.

(*c*) The London Clay flora is more closely linked with that of Indo-Malaya than with that of any other existing flora.

The final answer to these speculations can only be provided by extensive research on fossil floras from many widespread regions. At present the evidence is insufficient to furnish incontrovertible proof, but the balance of probability seems in favour of a remote origin of the Tethyan type of flora within a uniform palaeotropical belt in the early Cretaceous, and of an immediate origin of the London Clay flora by migration from Indo-Malaya between Cretaceous and early Eocene times.

The subsequent history of the London Clay flora and the reasons why it survived only in Indo-Malaya have been set forth by C. & E. M. Reid (1915), Reid & Chandler (1933), Chaney (1940, 1947) and others. When during the Oligocene the connection of the Tethys with the Indian Ocean was broken so that the former vast waterway became a huge land-locked Mediterranean, while the great transcontinental mountain barriers of Eurasia were being uplifted, progressive cooling of the climate in middle latitudes occurred, so that more temperate plants from the North gradually supplanted the former tropical ones of the Eocene. During this period final extermination was the fate of the Tethyan flora in Europe. With the shrinking of the Tethys a migration route to Asia no longer existed under favourable climatic conditions. The direct route to the tropics in the South was blocked by the combined barriers of East–West mountains and the East–West remains of the Tethys, as effectively as Northward migration had formerly been blocked by the vaster Tethyan ocean of late Cretaceous and Eocene times.

But in South-East Asia, as already stated, survival of the palaeotropical flora and its descendants was possible, for there is no reason to think that equatorial latitudes in that continent have ever passed through a phase when it could not have retained its tropical flora. Even when the more northerly parts of the palaeotropical belt became cooler, so that the tropical flora could no longer live in them, migration to more southerly regions was possible, thanks to the absence of East–West barriers and to the existence of North–South valleys and coastal plains.

Meanwhile it is likely that the Tethyan flora of Egypt, when more fully known, will reveal a far stronger African element than is found in the London Clay, cut off as this latter appears to have been from direct communication with the African continent throughout its history.

The affinities of unknown plants in the Egyptian fossil flora should therefore be sought among tropical and sub-tropical African genera of the present day as well as among those of South East Asia.

I wish to express my warmest thanks to Mr. W. N. Edwards for helpful suggestions and criticisms, and to Mr. F. M. Wonnacott of the Geological Department for much help in the preparation of the manuscript for the press.

## SYSTEMATIC DESCRIPTIONS

*Note.*—The specimens, with two exceptions, are from the Dano-Montian Lower Esna Shales of Egypt.

Those from Kosseir Area, Red Sea, were collected by Dr. M. I. Youssef, those from Kharga Oasis by Dr. M. Y. Hassan, to both of whom I am indebted for the opportunity to study these most interesting plants and for the generous gift to the British Museum of the figured specimens.

The other two horizons and localities represented are the Lower Danian of Farafra (*Palaeowetherellia*), and the Eocene beds of Wadi Rayan (*Thiebaudia rayaniensis* gen. et sp. nov.).

## MONOCOTYLEDONES

### Family NIPACEAE

### Genus ***NIPA*** Thunberg 1782

### ***Nipa burtini*** (Brongniart)

(Pl. 10, figs. 1–5; pl. 11, figs. 7–9)

1904. *Nipadites sickenbergeri* Bonnet, p. 499, figs. on pp. 500, 501.
1924. *Nipadites sickenbergeri* Bonnet: Kräusel, p. 36.
1939. *Nipadites sickenbergeri* Bonnet: Kräusel, p. 22, pl. 1, figs. 1–18, text-fig. 1.
1939. *Rubiaceocarpum markgrafi* Kräusel, p. 108, pl. 1, figs. 19–24.

For full synonymy see Reid & Chandler (1933 : 118).

LOCALITIES AND HORIZONS. North slopes of Mokattam, near Cairo; Middle Eocene. Gebel Atshan, Kosseir Area, Red Sea; Dano-Montian Lower Esna Shales.

DESCRIPTION AND REMARKS. The discovery of a small *Nipa* fruit in the Dano-Montian of Kosseir and the re-investigation of fruits named *Rubiaceocarpum markgrafi* Kräusel from the Middle Eocene of Mokattam made it necessary to re-study *Nipadites sickenbergeri* Bonnet from the same beds as *Rubiaceocarpum*.

As a result it can be stated with confidence that *Rubiaceocarpum* is a *Nipa* seed with outer integument preserved in part at least, and that it, and the seeds named *Nipadites sickenbergeri*, cannot be separated from *Nipa burtini* (Brongn.) in the present state of our knowledge.

This conclusion was forced by the evidence upon the writer who had started with the conviction that *N. sickenbergeri* was distinguished beyond question from *Nipa burtini* by its ribbed and furrowed seed. Moreover the opinion expressed by Reid & Chandler (1933 : 122) that the fossils should be referred to *Nipa* rather than to *Nipadites* is now re-affirmed.

In order the better to understand the fossils a further examination of the living *Nipa fruticans* was carried out. The following details may now be added to those recorded by Reid & Chandler (1933 : 122).

The hard compact endocarp when freed from the adherent pericarp (or sarcocarp) is more or less smooth but shows on its outer surface, in the parenchyma which covers it, impressions of stout longitudinal fibres. There is no conspicuous fluting or ribbing of this surface, but a tangled mass of finer fibres can be seen where the parenchyma is rubbed off. When abrasion is carried a stage further stout transverse fibres are exposed. These were observed in 1933. The locule shows conspicuous flattened transverse or oblique fibres and stout longitudinal ones overlying them which readily break away.

When an endocarp is cut transversely, a nut-like seed may fall free if the material is in a suitable state of preservation. This bears upon its surface conspicuous flutings due to narrow deep furrows in a parenchymatous layer. In the furrows there are remains of fibres which probably belong to the endocarp. They have usually been torn away, leaving empty furrows only on the surface of the seed. Some of the fibres branch or unite so that the furrows and intervening ridges are not aways absolutely straight and longitudinal, although this is their general alignment. On the flat or slightly convex broad ridges between the furrows can be seen impressions of the transverse or oblique flattened fibres which belong to the locule wall described above (Pl. 11, fig. 10).

In Reid & Chandler's description this coat of the testa was regarded as part of the endocarp because endocarp and testa are often fused. On the detached seed there is a deep narrow parallel-sided furrow (Pl. 11, fig. 12). This is formed by an incomplete longitudinal ridge or septum which projects into the locule from the whole length of the carpel wall. The large sub-circular or circular basal aperture giving access to a cavity in the endosperm is a conspicuous feature also, and is associated with the embryo. The outer pulpy integument of the testa is fairly easily scraped away, exposing a close-textured rather brittle, gummy or resinous inner integument with a smooth transversely striate outer surface of fine cells. Embedded in the surface of this coat are a few flat fibres which branch and anastomose to form a coarse network. The fibres lie obliquely, transversely, or more infrequently longitudinally (Pl. 10, fig. 6). On the inner side of the brittle inner integument is a raised network due to very fine fibres so arranged as to form fine transversely elongate meshes.

The inner integument follows fairly closely the contours of the endosperm, but is separated from it by a thin soft film of fine cells. When the endosperm has rotted, as may happen in specimens which have drifted in the sea for some time, the empty integuments of the seed may still remain attached firmly to the endocarp as it lies within the drupe, but the film of cells just described has usually gone so that only the network of fibres with transverse meshes covers the exposed surface. It is the internal cast of this coat with its fibres which shows the ornamentation described on seed-casts of *Nipa burtini* from the London Clay (Reid & Chandler, 1933, pl. 2, fig. 6).

No raphe or chalaza scar is visible on the interior of the inner integument in

Recent fruits, nor is their existence indicated by any change in the alignment of the fine fibrous network so far as I have been able to observe. When all the integuments are removed so that the actual endosperm is uncovered, a series of even finer furrows and ridges, like minute ruminations, are laid bare. At the apex and over the sides of the endosperm their orientation is clearly transverse (Pl. 10, fig. 6 ; Pl. 11, fig. 11). At the base they are coarser and the alignment more irregular, giving rise to small low rounded lobes of endosperm. Whatever the orientation, the small areas which they produce on the surface are more or less convex, especially when slightly weathered or abraded. The endosperm sometimes displays a few broad shallow longitudinal furrows or sinuosities at the lower end which gradually die out above (Pl. 11, fig. 12). They resemble the furrows sometimes seen in *Nipa burtini* and *Nipadites sickenbergeri*. On the exterior of the complete seed they are barely discernible, being obscured by the spongy outer integument. Nor are they usually apparent on the inner surface of the empty testa.

The astute observer Hooker in an editorial note (Le Maout & Decaisne, 1876 : 822) comments that the seeds are erect and anatropous. But for this observation I should not have suspected their anatropous character, for there is no more indication of a raphe on the outer surface of the testa than there is on the inner surface. Nevertheless examination of a detached endosperm-mass supports Hooker's statement, or at least gives evidence of comparable structures. After removal of the integuments a flat band of fibres was seen lying in one of the shallow longitudinal furrows of the surface. It extends upwards from the base almost throughout the length, follows a straight course, and is parallel-sided, quite different in character from the somewhat sinuous flat fibres in other furrows. That this is a definite structural feature, probably the raphe, is confirmed by the differentiation of a band of endosperm immediately beneath it. In this position there are small irregular rounded " ruminations," not transversely elongate ones as elsewhere, and some indication of longitudinal alignment is given by a tendency for longitudinal cracks to form (Pl. 11, fig. 11). Somewhere in this band the fibres must enter the endosperm and pass to the chalaza. But the point of entry is so inconspicuous that it is hidden by the irregularities of the " ruminate " surface. Nevertheless a corresponding structure shows clearly in some fossil material, as will be described later.

From the details given above it is fairly clear that the appearance of a fossil *Nipa* must vary considerably with the coat which happens to have been preserved or exposed. This depends partly on the mode of preservation of the fossil. Thus an internal seed-cast may show the structure of the endosperm as in the Egyptian *Nipa*, or it may merely be a cast of the inner integument formed after the endosperm had decayed as in many London Clay seeds.

Any seed having the ridged outer integument preserved would have the distinctive appearance of *Rubiaceocarpum*, further details of which are given later. In a broken fruit some layer or layers of the endocarp may show, as in many fruits from the London Clay, and in a small Dano-Montian fruit from Egypt. In the London Clay fruits wear and tear has often exposed the inner layers of endocarp with flat transverse fibres described in 1933. By far the most common specimens at Sheppey and Herne Bay are fruits (perfect or imperfect), showing stout fibres embedded in the spongy tissue of the sarcocarp. Rarely is the epicarp preserved, and then only in fruits freshly removed from the matrix. It quickly cracks and falls to pieces on exposure to air.

It seems scarcely necessary to repeat detailed descriptions of the fossil fruits and seeds which have already appeared in published work (Reid & Chandler, 1933 : 119 ; Kräusel, 1939 : 22 ; Seward & Arber, 1903, etc.). Other references will be found in the synonyms listed by Reid & Chandler (1933 : 118).

The question inevitably arises once more, " How many fossil species can be distinguished in the deposits with which we are now concerned ?"

It must be remembered that whereas the London Clay fruits and seeds are relatively uncrushed, the Egyptian ones have often undergone an excessive amount of deformation by crushing and there appear to be no valid and consistent grounds for separating *Nipa burtini* and *Nipadites sickenbergeri* as distinct species. The longitudinal ridging and furrowing of the seed-casts, or its absence, although it was supposed by Bonnet to be of specific value, cannot really be used in diagnosis, for although smooth seed-casts are common in the London Clay, furrowed ones may also occur. Moreover both kinds are found in the Egyptian Eocene (Bowerbank, 1840, pl. 4, fig. 1; pl. 5, fig. 1 ; Kräusel, 1939, pl. 1, figs. 11–13).

Again in the Egyptian casts the furrows may be few and slight (V.13695) or fairly conspicuous, or in some cases, overemphasized by crushing.

The other chief difference which occurs in some cases between fossils from the two localities lies in the size. But differences in size are no more satisfactory than furrowing, as a reason for specific separation. It is true that the majority of *Nipa burtini* fruits and seeds from the London Basin are smaller than the majority of the seeds from Egypt, and that they vary greatly in appearance. Yet large nuts do occur in the London Clay (Bowerbank, 1840, pl. 5, fig. 1), while very large fruits and seeds occur in the Belgian strata (Seward & Arber, 1903). On the other hand the small fruits from the London Clay are indistinguishable from a Dano-Montian fruit from Kosseir (Pl. 10, figs. 1, 2). Perhaps the predominance of small forms in one area and large in another may be due to the sorting effects of specific gravity rather than to systematic differences. The associated fruits of other families at Sheppey and Herne Bay are on the whole fairly small.

The following table shows minimum and maximum sizes of fossil Nipas from previously published records. It must be remembered, however, that a far larger number of specimens are known from the London Clay than from the other deposits and they include many immature or abortive fruits.

| London Clay | Belgian Eocene | Egyptian Eocene |
|---|---|---|
| *Fruits :* | | |
| Length, 1 to 18 cm. | 7·5 to 21 cm. | Not known |
| Breadth, 1·3 to 12 cm. | 3 to 15 cm. | „ |
| *Seeds :* | | |
| Length, 2 to 8·9 cm. | 9 to 10 cm. (commonly 8·5 to 9 cm.) | 7·5 to 11 cm. (commonly 8·5 or 9 cm.) |
| Breadth, 1·3 to 7 cm. | 9 cm. (commonly about 7 cm.) | 3·4 to 12·3 cm. (commonly about 5 to 7 cm.) |

Thus whether furrowing or size be considered, there appear to be no sharp lines of demarcation between species from the localities with which we are concerned.

If furrowing and size cannot be used as a basis for separating species—and it is difficult to see how they can when every gradation may occur in these characters—there are no other grounds obvious on which the diagnosis of more than one species can be based.

Certainly the differences between the Nipas from the two areas under review are no greater than the differences among individual specimens in the London Clay itself (cf. Bowerbank, 1840, pl. 4, fig. 1 ; pl. 5, fig. 1). Yet there is no reason whatsoever for creating more than one species in this deposit.

A few additional observations on the Egyptian nuts may not be out of place here. Kräusel's figured specimens are largely seed-casts and might be expected to show endosperm structure. Unfortunately the small scale of the figures does not display such fine details except in his pl. 1, fig. 8, where transversely aligned endosperm cells are clearly seen around the basal scar. Endosperm structure is also clearly visible in two casts from Mokattam in the British Museum (V.13240 and V.13695 ; Pl. 11, figs. 7, 8).

The variable and considerable amount of compression of the seeds must be stressed, for some are almost reduced to thick concavo-convex lenticles (V.13240). Inevitably this crushing increases the diameter. V.13239 is obliquely distorted, the basal aperture having been forced into a basi-lateral position (Pl. 10, fig. 3).

As in the living, so also in the fossils, endosperm may show features not discernible on the interior of the testa represented by internal casts. V.13240, in addition to the typical transverse pattern of endosperm ridges (Pl. 11, fig. 8), shows on its flatter surface a band of elongate, longitudinally aligned endosperm cells which by comparison with the living have structural significance, probably indicating the position of the raphe. Towards, but well below, the apex a radial arrangement of the endosperm on this band suggests the point of entry into the endosperm of the fibres from the raphe (Pl. 11, fig. 7). On the more convex surface of this specimen, the coarse network of fibres seen in the living between the two integuments of the testa are faintly impressed (Pl. 10, fig. 5).

V.13239 has a mosaic pattern all over the surface. This may be the impression of a cracked testa which has peeled. But the important feature of this specimen is that sub-apically the cast shows a deep, small, funnel-shaped opening towards which fibre-impressions converge, and into which they pass (Pl. 10, fig. 4). Here the entry of the raphe fibres is clearly indicated. V.13695 shows a similar but more obscurely preserved radiating structure.

Thus these specimens illustrate a well-established fact, that owing to the maceration that fossils have frequently undergone, they may display structures which are more difficult to demonstrate in Recent material.

We must now return to the specimens named *Rubiaceocarpum markgrafi* Kräusel. As already stated on p. 159 these appear to be seeds (abnormally short and broad) with outer integument preserved. They have undergone considerable lateral compression.

Their form can be matched among the *Nipa* seed-casts illustrated by Kräusel

(1939, pl. 1, cf. figs. 8, 21; 18, 24; 16, 24; 17, 20). I have been able to examine the specimen illustrated in Krausel's fig. 24, which shows the base of the seed with its large aperture. A very interesting feature is a broad flat fibre band which half encircles the seed in the plane of symmetry (Pl. 11, fig. 9*f*). This resembles the raphe fibre described above in *Nipa fruticans*, although seed and fibre are on a larger scale. The fact that it is visible at the surface of the specimen must mean that some measure of abrasion had removed part of the spongy parenchyma. The superficial impressions of the transverse fibres of the endocarp have also been destroyed at the same time, traces only of them being visible in a few of the deeper furrows of the outer integument.

We may ask what relationship does this ribbed entity bear to its living analogue? It appears to be an internal cast of a hollow mould left by a seed which subsequently decayed. The filling of the hollow with limestone resulted in the characters impressed on the mould being reproduced on a cast, much as sealing-wax poured into the hollow mould of any fossil will reproduce its solid form. An actual replacement of the seed itself cell by cell would have given a far sharper representation of it, and in places at least would have provided evidence of cell-structure.

The ribbed seed shown by Kräusel (1939, pl. 1, figs. 20, 21) perhaps retained even more of the outer integument, for there are suggestions of transverse fibre impressions at the base of fig. 21, and the raphe band appears to be only partly uncovered.

The longitudinal striation on the ridges in Kräusel's pl. 1, fig. 1, may indicate that part of the outer integument of the testa is still present on this cast, which he referred to *Nipadites*. But suggestions such as this can only be verified by examination of the specimens themselves.

Reid & Chandler (1933 : 122) gave reasons for referring the London Clay fossils to *Nipa* rather than to *Nipadites*. They appear still to hold good. The most outstanding difference between living and fossil is the presence of the short longitudinal septum, which by partial subdivision of the locule in *N. fruticans* produces the only constant deep and conspicuous longitudinal furrow on the seed. This septum and furrow are absent in all the fossils. Nevertheless so closely identical with the living is the structure of the fossils in all other respects (even in smallest details) that the presence or absence of the septum still appears to the writer to have specific rather than generic value. Probably however, the real meaning of this character can only be decided by a detailed study of the developing ovary. It may, or may not, have a connection with the suppression of two out of the three original locules or ovules. In the meanwhile it is suggested that the name *Nipa* be used for the fossils.

## DICOTYLEDONES

### Family ANONACEAE

### Genus ***ANONASPERMUM*** Ball *emend* Reid & Chandler, 1933

### ***Anonaspermum aegypticum*** n. sp.

(Pl. 11, figs. 13–15)

DIAGNOSIS. Seed-cast oval or oboval in outline, much compressed with slight median depression ; rumination ridges close and narrow, extending from the depression to the margins, diverging from the depression at the distal end, occasionally forking near the margin, with a few short intermediate ridges. Four-partite in transverse section. Thickness only about half the greatest diameter in the plane of symmetry (15·5 mm.).

HOLOTYPE. A seed-cast, distal end, with testa almost entirely abraded (Pl. 11, figs. 13–15). Brit. Mus. (N.H.), No. V.31106.

LOCALITY AND HORIZON. Gebel Atshan, Kosseir Area, Red Sea ; Dano-Montian Lower Esna Shales.

DESCRIPTION. The unmistakable internal cast of a seed of Anonaceae showing typical ruminate albumen and marginal encircling band of raphe and chalaza (Pl. 11, figs. 13, 14). The hilar half of the seed is missing. The surviving fragment represents the distal end, which appears to have been severed from the proximal only a short distance above the middle of the specimen. The cast was originally oval or oboval in outline, bisymmetric, somewhat compressed at right angles to the plane of symmetry, anatropous with encircling raphe in the plane of symmetry. The raphe begins to broaden on one side where it merges into the linear chalaza (Pl. 11, figs. 13, 14 *ch.*). It completely fills the slight marginal groove at the edge of the albumen. Albumen having a median depression on each broad surface, ruminations forming narrow close ridges from the margin of the seed to the median depression. The ridges diverge from the end of the depression to the apex or distal end of the seed. The inner ends of opposite ridges do not unite at this point to form a series of curves as in *Anonaspermum commune* Reid & Chandler (1933 : 184, pl. 5, figs. 14–17). Short ridges of varying length sometimes arise at the margin and are interposed between the longer ones. Occasionally one of the longer ridges may divide into two towards the margin of the seed. The transverse section exposed on the fractured surface shows a four-partite arrangement of the albumen (Pl. 11, fig. 15). In the slight depressions in the middle of the broad surfaces part of the fibrous layer of testa is preserved (Pl. 11, fig. 13). On the four-partite sectioned surface oblong cells arranged in transverse rows at right angles to the plane of symmetry of the seed can be seen. The rows are about 0·028 mm. broad. The cells are partially obscured by sinuous fine striations lying parallel in a general way with the plane of symmetry. Parts of the ruminations as seen on the fractured surface of the seed are obscured by a thin brown mineral film which bears the impression of a thin but rough coat, the cells of which lie at right angles to the plane of symmetry. It represents the filmy inner integument which penetrated between the plates of albumen as in living seeds.

Actual length of seed preserved, 10 mm.; estimated length of complete seed, about 22 mm. Maximum diameter actually preserved in plane of symmetry, 14 mm.; probable measurement in the complete seed, about 15 to 15·5 mm. Diameter at right angles to plane of symmetry, 7 (at the centre) to 7·5 mm. (at each side).

REMARKS. The seed was clearly larger than any described from the London Clay, about twice the size of the largest there recorded. It was also relatively thinner at right angles to the plane of symmetry than any London Clay species with albumen forming superficial ridges. Similar divergence of the ruminations at the distal end is seen in *A. rugosum* and *A. pulchrum* Reid & Chandler (1933 : 186, 187, pl. 5, figs. 21–27), but not in *A. commune* and *A. rotundatum* Reid & Chandler (1933 : 184–187, pl. 5, figs. 14–20).

Although imperfect, this solitary specimen appears to be sufficiently distinctive to merit a specific name. It is described as *Anonaspermum aegypticum*. The family Anonaceae is almost exclusively tropical today, occurring in both hemispheres. It is recorded from both hemispheres in Eocene times also.

## Family EUPHORBIACEAE

### Genus ***LAGENOIDEA*** Reid & Chandler *emend.*

Since the first description of this genus was published (Reid & Chandler, 1933 : 493–497) a few small but important new facts have come to light which make it necessary to correct the diagnoses and descriptions then given. The information was derived from additional London Clay material of *Lagenoidea trilocularis*. The diagnosis should now read :

Fruit a superior, syncarpous, loculicidal and septicidal capsule, two to four-loculed, locules single-seeded. Pericarp thick, formed of radially aligned cells, seeds pendulous, radially compressed, anatropous, raphe ventral, chalaza basi-ventral.

TYPE SPECIES. *L. trilocularis* Reid & Chandler.

The recent discovery that the seeds are pendulous with ventral raphe now makes it possible to refer the genus *Lagenoidea* to the family Euphorbiaceae. Formerly such a relationship was considered impossible, for the seeds were then believed to be erect and orthotropous owing to the fact that the raphe is slender and difficult to detect when it is preserved at all.

The shape of the fruit and the combined loculicidal and septicidal dehiscence is typical of the Euphorbiaceae. This was recognized by Ettingshausen when he labelled one specimen (V.23129) *Euphorbiophyllum eocenicum* (see Reid & Chandler, 1933 : 495, pl. 29, fig. 6). This specimen was never described or figured as such, hence the inappropriate name *Euphorbiophyllum* need not be retained for these fruits. It has not yet been possible to connect them with a living genus, but the relationship must be sought among those sections of the Euphorbiaceae with single-seeded locules having locule-linings formed of complicated interlocking cells. Attenuated obovate seeds are rare in the family but obovate seeds may occur, e.g., in *Chaetocarpus* where the seeds may remain attached to the inner angle of the carpel wall when the external valves have fallen away.

### ***Lagenoidea trilocularis*** Reid & Chandler

(Pl. 12, figs. 16–20)

1933. *Lagenoidea trilocularis* Reid & Chandler, p. 493, pl. 29, figs. 1–18.

The revised diagnosis of this species based on London Clay material as stated above should read:

*Fruit:* Sub-globular, three- (rarely four-) loculed; capsule splitting loculicidally and septicidally into six (rarely eight) segments. Length, 7 to 14 mm.; diameter, 8 to 23 mm.; length of locule-cast (= seed), 3·5 to 4·5 mm.; greatest diameter, 2 mm.; least diameter, 1 mm.

LOCALITY AND HORIZON. Gebel Atshan and Gebel Durvi, Kosseir Area, Red Sea; Dano-Montian Lower Esna Shales.

MATERIAL. Two fruits, one with hollow interior. Brit. Mus. (N.H.), Nos. V.31107–08.

DESCRIPTION AND REMARKS. Two fruits, neither of which show internal structure. One (Pl. 12, figs. 16–18) shows a thin wrinkled epicarp partly hiding the surface of the capsule, but the six segments can be clearly distinguished. A sub-circular basal scar indicates the former extent of the calyx (Pl. 12, fig. 17). Length of fruit, 10 mm.; transverse diameter, 9 by 11 mm.

The second fruit (Pl. 12, figs. 19, 20) also shows the six valves and basal scar, but its surface is somewhat encrusted and is therefore rather obscure. The interior is hollow, while there is a hole at the attachment through which the seeds may be presumed to have escaped. Length of fruit, 11 mm.; diameter, 14 by 12·5 mm.

### ***Lagenoidea bilocularis*** Reid & Chandler

(Pl. 12, figs. 21–23)

1933. *Lagenoidea bilocularis* Reid & Chandler, p. 496, pl. 29, figs. 19–27.

LOCALITY AND HORIZON. Gebel Atshan, Kosseir Area, Red Sea. Dano-Montian Lower Esna Shales.

MATERIAL. Two typical fruits. Brit. Mus. (N.H.), No. V.31109.

DESCRIPTION. Two sub-ovoid somewhat laterally compressed fruits showing six external longitudinal grooves delimiting the valves and septum. The narrow median opposite segments between the pairs of lateral segments mark the edges of the septum. The pairs of end segments are bounded by planes of loculicidal and septicidal splitting. As in the London Clay fruits of this species the pairs of valves may be presumed to overlie the two locules.

The stylar scar is seen at the narrow end in both fruits and the attachment scar is preserved at the broad end in the smaller specimen. Unfortunately the internal structure is not exposed. There can be no doubt however that the fruits are identical with the London Clay species *Lagenoidea bilocularis* Reid & Chandler.

Length of the two endocarps, 11 and 9·5 mm.; greatest diameters, 11 and 9 mm.; least diameters, 6 and 5·5 mm. respectively.

### Family EUPHORBIACEAE ?

### Genus ***PALAEOWETHERELLIA*** nov.

DIAGNOSIS. Fruit sub-globular, syncarpous, with more than five carpels; dehiscence loculicidal and septicidal, locules radially arranged, tangentially compressed; placentation axile; seeds solitary in each locule, occupying part only of the plane of the locule; pendulous by long arched funicles which arise some distance below the apex of the fruit. Pericarp parenchymatous. Seeds slightly inflated, obovate in outline, beaked at the micropyle, anatropous with ventral raphe. Testa one cell thick, formed of equiaxial cells.

TYPE SPECIES. *P. schweinfurthi* (Heer).

### ***Palaeowetherellia schweinfurthi*** (Heer) Chandler

(Pl. 12, figs. 24–30; Pl. 13, figs. 31–38; Pl. 14, figs. 39–47; Pl. 15, fig. 48; Text-fig. 1)

1876. *Diospyros schweinfurthi* Heer, p. 6, pl. 1, figs. 1–10.
1876. *Royena desertorum* Heer, p. 10, pl. 1, figs. 11–16.
1889. *Diospyros schweinfurthi* Heer: Schenk, p. 745, text-fig. $384^{7-13}$.
1889. *Royena desertorum* Heer: Schenk, p. 745, text-fig. $384^{14-18}$.
1939. *Diospyros schweinfurthi* Heer: Kräusel, p. 106, pl. 2, figs. 9, 10; text-fig. 32.
1939. *Royena desertorum* Heer: Kräusel, p. 106.

DIAGNOSIS. Fruit shorter than broad, 6 to 9, 10 or even 12-loculed. Funicles arising from the axis at about one-third to one-half the length of the fruit from the apex, passing between the closely opposed surfaces of the locule above the seed. Seed so obliquely placed as to lie almost transversely with the hilum upwards towards the circumference of the fruit, and the ventral margin parallel with the arched funicle. Fine parenchyma which forms the bulk of the carpel wall enclosing numerous patches of coarser cells very liable to decay associated with a system of fibres near the surface of the endocarp. Diameter of endocarp, 17 to 22 (or ? 24) mm.; length about 7·5 to 10 mm. Maximum length of fruit with exocarp preserved, 14 mm.

NEOTYPE. A nine-loculed fruit (Pl. 13, figs. 31–37). Figured Kräusel, 1939, pl. 2, figs. 9, 10 ; text-fig. 32. Brit. Mus. (N.H.), No. V.12985.

LOCALITIES AND HORIZONS. Farafra, Egypt ; Lower Danian (Upper Cretaceous). Gebel Tarawan and Gebel Um-el-Ghanaim, Kharga Oasis, Egypt ; Dano-Montian Lower Esna Shales. Gebel Atshan, Gebel Durvi and Abu Tundub, Kosseir Area, Red Sea ; Dano-Montian Lower Esna Shales.

DESCRIPTION. *Fruit:* Having an exocarp (leathery ? but usually abraded) about 1·6 mm. thick, its surface more or less smooth but the details of its structure obscured by mineral incrustation (Pl. 12, fig. 27 ; Pl. 14, figs. 42, 43). It encloses a syncarpous multilocular endocarp, circular or sub-circular in outline, sometimes slightly angled over the locules, depressed dorsiventrally, usually somewhat flattened at the apex, either slightly pointed below or somewhat excavated (Pl. 12, figs. 24–26 ; Pl. 13, figs. 31, 32).

The style base may be marked by a small inconspicuous scarcely prominent circular scar (Pl. 13, fig. 31), but this is not usually apparent. External surface with radial ridges or sutures which correspond with the locules. Alternating with them are less conspicuous ones which overlie the septa ; they are not invariably seen, and are most marked in much abraded specimens or in those which have started to split septicidally (Pl. 12, figs. 25, 29, 30). Dehiscence conspicuously loculicidal, less obviously septicidal. Possibly the septicidal planes of weakness are cemented by infiltration of mineral substance as they are normally so inconspicuous. Carpels 6 to about 12, radially arranged about the axis of the fruit (Pl. 12, figs. 24–26 ; Pl. 13, figs. 31, 32), unequally developed in some specimens so that complete fruits may show perfect or imperfect radial symmetry. V.12985, for example, shows unequal development at opposite ends of one diameter, two of the smaller carpels are evidently abortive, but their existence is clearly revealed by a longitudinal fracture of the fruit (Pl. 13, figs. 33–36). One of Heer's transversely sectioned specimens (1876, pl. 1, fig. 9) in which he only recognized 8 locules clearly shows 9 in the figure, 2 being abortive or ill-developed. Up to the present the least number of carpels seen is six (Pl. 12, figs. 24, 25). Fibres of the fruit axis fused with the surrounding parenchyma not occupying a distinct central canal. Locules extend from the axis to the periphery of the fruit, but are tangentially compressed and so completely flattened around their edges that the two flat surfaces are contiguous. The seeds are neither as long nor as broad as the locules. It is only where the seed actually lies that there is a slightly inflated cavity equal to the thickness of the seed (Pl. 13, figs. 32–36 ; Pl. 15, fig. 48). Placentation axile. Seeds solitary, suspended by long arched funicles which spring from the axis at about one-third or one-half of the length of the fruit from the apex. From the point of emergence of the funicle from the axis (Pl. 13, figs. 33–37 ; Text-fig. 1D) to the point where it passes into the seed at the hilum it lies within that part of the locule where the opposed walls are contiguous. The longer axes of the seeds lie at an angle of 60° or thereabouts to the axis of the fruit, hence the position of the seeds is oblique or almost transverse in the fruits. As this is a consistent feature it must be original. Owing to this peculiarity, the dorsal surface of the seed lies towards the base of the fruit, the hilar end is directed outwards and upwards, the distal end lies close to the lower end of the fruit axis, and the ventral margin is uppermost, lying parallel with the long arched oblique funicle.

Pericarp of three layers: (1) a leathery (?) exocarp of fine parenchyma whose surface is obscure, but in section it can be seen in one place to be formed of rounded more or less equiaxial cells about 0·028 mm. in diameter. (2) A compact parenchymatous coat which constitutes the main thickness of the endocarp. It is greatly thickened in the part of the fruit between the flattened margins of the locules. The outermost part of the endocarp is formed of close fine parenchyma which is rather readily abraded. Superficially, when the coat is weathered, the cells can be seen to be arranged in radiating groups. Possibly there is a fibre at the centre of each group. Differential weathering of this coat produces a series of rugosities having the effect of a coarse network, the centre of each radial group being sunk below the general level of the surface. Beneath the layers of radially grouped cells comes the main thickness of the endocarp. It is formed of equiaxial cells about 0·02 mm. in diameter. Within it are numberous patches of coarse angular parenchyma, with cells about 0·05 to 0·1 mm. in diameter, developed most conspicuously near the outer surface of the coat. These patches also may have a thin fibrous core fed by fibres visible near the periphery on the flat surfaces of the loculicidally fractured carpels (Pl. 12, fig. 30; Pl. 13, fig. 35). Here loops are seen from which branches are directed inwards to the centre of the endocarp, while more numerous and finer branches are directed outwards to its external surface.

V.12985 had laid long exposed before fossilization, and the coarse parenchyma patches have decayed more readily than the more compact tissue which surrounds them. Their decay has produced deep funnel-shaped cavities with circular orifices which form a conspicuous feature at the surface of the endocarp. They are best shown on the lower surface, where they occur in more or less longitudinal rows (Pl. 13, fig. 32). The whole surface of this specimen (as preserved) has been highly polished by the abrasion it has undergone.

(3) The innermost carpellary coat is a smooth locule-lining formed of small cells arranged so as to produce straight or slightly sinuous or criss-cross lines or striations with a general transverse or oblique orientation. The distance between the striae is about 0·02 mm. The striate lining is seen to the left of the axis in Pl. 13, fig. 36, and is more clearly visible on the specimen itself and on the surface of the abortive locule-cast.

There is some reason to think that that part of the thick parenchymatous coat which was in contact with the locule-lining was rather spongy in texture, or that it was at least softer and less resistant to decay than the layers outside it. In places it is partially decayed, while in other places it appears obscurely columnar in transverse section (Pl. 13, fig. 35, to the left of the fertile locule-cast). It clings in patches to the locule-cast, giving the appearance at first sight of a warty testa formed of fine angular, parenchymatous cells (Pl. 13, fig. 35; Pl. 14, fig. 41). But careful scrutiny reveals its true nature. The decay is most conspicuous around the axis at the base, exposing the locules and seeds in some specimens (Pl. 12, fig. 26; Pl. 13, fig. 32). Length of fruit, 7·5 to 9·5 mm.; transverse diameter, 17 to at least 22 (? 24) mm. Length of V.12985, 8 mm.; diameter, 19 mm. Length of specimen shown in

Pl. 14, figs. 42, 43, with exocarp preserved, 14 mm.; estimated diameter, 24 by 17 mm. Length of another fruit, 10 mm.; diameter, 22 mm.

*Seeds* (Pl. 13, figs. 33, 35, 37; Pl. 14, figs. 40, 41, 43–47; Pl. 15, fig. 48): More or less obovate in outline, very slightly inflated, with a small beak-like projection at the hilar end which carries the micropyle. This organ is indicated by the radial alignment of the cells at its tip. That the radicle probably lay within the beak is suggested by its shape. The general symmetry indicates an anatropous seed with hilum in the concavity which delimits the "beak" from the main body of the seed, i.e., closely adjacent to the micropyle. Here the funicle is seen to enter the seed (cf. Pl. 12, fig. 28; Pl. 13, fig. 35). Raphe marginal, ventral, indicated by the form of the seed as well as by a shallow marginal groove at the rounded end opposite to the micropyle. The groove ends on the dorsal surface. Its termination probably indicates the position of the obscure chalaza.

On the rounded end of the best developed seed exposed by abrasion within a locule-cast of V.12985 the chalaza is probably marked by a small deep depression in the same position (i.e., at the lowest point of the seed as it lay in the fruit). If so this is the cast of the raphe fibres, where they turn sharply inwards to enter the seed or albumen.

Testa apparently only one cell thick, since the cells of the external and internal impressions appear to agree exactly in size and character. It was formed of equiaxial polygonal angular cells about 0·025 to 0·03 mm. in diameter, convex externally (as shown by the concave external impressions on a small fragment of external cast seen in the specimen figured in Pl. 14, figs. 42–47), concave internally (shown by the convex impressions on the internal casts of the seed figured in Pl. 14, figs. 39–47). Dimensions of seeds: Length, 5·5 to about 7 mm.; breadth, 4 to 5 mm.; thickness, 1 to 1·5 mm.

REMARKS AND AFFINITIES. In examining and interpreting mineralized fruits it is necessary to remember that mineral substance in solution may percolate through all incipient fissures as well as into actual cavities. On evaporating and hardening it may then form a cement which prevents or hinders separation of parts along natural planes of weakness. But in that the film of cement may often be incomplete, indications of natural dehiscence can usually be detected. Thus in *Wetherellia* (Reid & Chandler, 1933: 251), while many specimens were so cemented that their loculicidal dehiscence was concealed, the fruits were found in such large numbers that plenty of evidence as to their natural manner of splitting was available. In the fossil just described septicidal dehiscence may be obscured in a similar way. The mineral cement may cause adhesion of surfaces and tissues which in life, or at least after maceration, whether natural or artificial, would separate readily. For example, in *Palaeowetherellia*, a locule-cast may simulate a seed (which it covers and conceals), and patches of endocarp adhering to the cast but torn from adjacent tissues may look like testa (cf. Pl. 13, fig. 35; Pl. 14, fig. 41). Again thin films of cement between delicate tissues may reproduce as external or internal impression coats which could scarcely have escaped destruction, e.g., the delicate one-cell thick testa of *Wetherellia* and *Palaeowetherellia*.

*Palaeowetherellia* is now known from more than a dozen specimens. In addition to those figured by Heer (1876) as *Diospyros*, ten more, five of which are incomplete, are now available. These will be catalogued below with details of any special features they show and a note of the place of origin.

The best preserved for study was described and figured by Kräusel (1939 : 106, pl. 2, figs. 9, 10 ; text-fig. 32) as *Diospyros schweinfurthi* Heer. Certain of its characters, including the number of locules, were obscure at the time, but have since been clearly shown by the beautiful section (largely a natural fracture surface) now exposed (cf. Pl. 13, figs. 33–37). On this section most of the newly recorded details are based. Two other specimens from the Kharga Oasis have yielded additional data, thanks to their broken condition, and have made it necessary to unite *Diospyros schweinfurthi* Heer and *Royena desertorum* of Heer as a single species (cf. p. 176). Other fruits or fragments from Kosseir throw light on the variation in the number of locules, the branching of fibres of the endocarp, mode of dehiscence, variations of size, and character of exocarp.

The new evidence makes it impossible any longer to refer this species to the family Ebenaceae in spite of some superficial resemblances to *Diospyros*. In this genus the soft pulpy fruit breaks irregularly ; its radially arranged locules (with coarse striae) have no flattened area where the two opposed surfaces are in contact. The seeds are pendulous on short funicles which spring from the upper inner angles of the locules arising at the top of the fruit axis (Text-fig. 1A). The anatropous seeds have a conspicuous superficial *dorsal* marginal raphe which does not terminate at the chalaza (i.e., at the opposite end of the seed to the hilum) but is continued along the ventral margin so as to encircle the seed. It gradually tapers, dying out finally close to the hilum. The seeds lie vertically in the locules with their ventral margins parallel with and close to the axis. They are not beaked like those of the fossil but the terminal micropyle usually leads into a large conspicuous canal produced by incurving of the testa. The radicle of the embryo occupies this canal, which on an internal cast of the seed would appear as a conspicuous deep depression or pit (Text-fig. 1E) with a projection from its base representing the cast of the radicular pocket. Similar features are characteristic of *Royena*, which resembles the fossil even less than *Diospyros* in the form and fewness of its seeds. One other characteristic may be noted, namely the cell-structure. In *Diospyros* the testa cells, while they may be similar in style to those of the Egyptian fossil, are *convex* internally, so that on an internal seed-cast they would produce concave instead of convex impressions. Unfortunately it has not yet been possible to find any living closely allied genus, although a suggestion will be made below as to family relationship. But there can be no doubt at all that *Palaeowetherellia* closely resembles the fossil genus *Wetherellia* Bowerbank from the London Clay in its form, placentation, locule characters, seeds, and cell-structure, and in the tendency for dissolution of the carpel to occur at the centre which allows the seeds to escape through the gaps thereby produced—a point noted by Bowerbank in describing *Wetherellia*. Similar decay may be seen in crab apples which have lain long on the ground in winter. A detailed description of *Wetherellia variabilis* was given by Reid & Chandler (1933, 251, pl. 9, figs. 7–22). A second species—*W. dixoni* (Carruthers)—has since been recognized from the Cuisian (?)—or it may be Lutetian or Auversian—of Selsey.

Its full description awaits publication. The characters of these two species of *Wetherellia* are summarized in a table below.

| | *Wetherellia variabilis* Bowerb. | *Wetherellia dixoni* (Carr.) |
|---|---|---|
| *Fruit :* | A syncarpous 2 to 5-loculed septicidal capsule or schizocarp, later splitting loculicidally. Sub-globular to ovoid with length equal to, greater, or less than the diameter. Smooth, ribbed, or angled externally. | A syncarpous 5 to 7 (or more ?) loculed capsule splitting septicidally and loculicidally. Sub-globular but somewhat dorsiventrally compressed. Longitudinally ribbed externally. Septal fibres apparently give rise to hollow external spines. |
| *Locules :* | Radially arranged around a central axis which extends throughout the length of the fruit. Tangentially compressed so that the opposed walls are contiguous except where the seed lies. | As for *W. variabilis.* |
| *Placentation :* | Axile ; solitary seeds suspended on long arched funicles which spring from the axis at a point about one-third or one-quarter of the length of the fruit from the apex. The funicles lie within that part of the locule where the opposed walls are contiguous. | As for *W. variabilis* except that the funicles spring from the axis at a point about one-sixth to two-sevenths of the length of the fruit from the apex. |
| *Seed :* | Slightly oblique, with the distal end nearer to the axis than the proximal. | As for *W. variabilis*, but the seeds somewhat broader in proportion to their length. |
| *Pericarp :* | Of thick angular parenchyma. Locule-lining smooth and shining, obliquely or transversely and finely striate. | As for *W. variabilis.* |
| *Dimensions of fruit :* | Length, 12 to 20 mm. Diameter, 12 to 24 mm. | Length, 4 to 7 mm. Diameter 13·5 to 15 mm. (somewhat dorsiventrally crushed). |
| *Seed :* | Scarcely inflated, elongate obovate in outline ; slightly beaked at the narrow hilar end, anatropous ; hilum terminal, raphe ventral, micropyle adjacent to the hilum ; chalaza small and inconspicuous at the opposite end to the hilum.<br>Testa thin, a single layer of angular equiaxial cells convex externally, concave internally, 0·03 to 0·05 mm. in diameter. | As for *W. variabilis*, but somewhat shorter and broader. Raphe fibres not actually seen.<br>Testa not seen. |
| *Dimensions of typical seeds :* | 12 × 3·75 × 1·5 mm. | (1) 5·5 × 4 × 1 mm.<br>(2) 7 × 4·75 × 1·5 mm. |

It may be noted that the parenchymatous tissues of both *Wetherellia* and of the Egyptian fruits is evidently very liable to decay, for partial destruction of the centre of the fruit has occurred in both so that the locules are exposed, allowing the seeds to escape. Consequently locules which have not dehisced in the normal way may be empty.

While therefore *Wetherellia* and the Egyptian fossils show a striking measure of agreement such as suggests a family relationship, their characters are sufficiently distinctive to indicate a generic difference between them. The name *Palaeowetherellia* is here suggested for the Egyptian fruits, which thus become *Palaeowetherellia schweinfurthi* (Heer).

The distinctions so far as they are known at present may be summarized in tabular form.

| *Wetherellia* | *Palaeowetherellia* |
|---|---|
| Septicidal capsule or schizocarp, also splitting loculicidally. Locules 2 to 7 (or more ?). | Loculicidal capsule also splitting septicidally.<br>Locules 6 to about 12. |
| Long arched funicles springing from the axis at one-sixth to one-third of the length of the fruit from the apex. | Long arched funicles springing from the axis at one-third to one half the length of the fruit from the apex. |
| Seed lying slightly obliquely in the locule with the distal end nearer to the axis than the proximal. | Seed so obliquely placed as to be almost transverse, with the proximal end towards the outer edge of the fruit and the distal end near the lower end of the axis. |
| Seeds scarcely inflated, oval to elongate obovate in outline, beaked at the narrow end. Hilum terminal. | Seeds slightly inflated, obovate in outline, beaked at the narrow end. Hilum almost terminal just below the beak on the ventral margin. |

In 1933 Reid & Chandler referred *Wetherellia* to the family Linaceae but it is necessary to correct this ascription on the following grounds:

(1) More than five locules are now known to occur in undoubted *Wetherellia* (*W. dixoni*).

(2) As noted in 1933 the coat of *Hugonia* (Linaceae) with which *Wetherellia* was compared is fibrous, that of *Wetherellia* and of *Palaeowetherellia* is consistently parenchymatous with a few scattered fibres.

(3) The seed in *Hugonia* occupies more of the locule than the seed of *Wetherellia* or *Palaeowetherellia*.

(4) The funicle is short and straight in *Hugonia*, not long and arched as in *Wetherellia* and *Palaeowetherellia*.

(5) Polygonal cells of the testa are much finer in *Hugonia* than in *Wetherellia* or *Palaeowetherellia*.

(6) The chalaza of *Hugonia* forms a large conspicuous scar unlike the inconspicuous scarcely distinguishable chalaza of *Wetherellia* and *Palaeowetherellia*.

Taken together these differences appear on maturer reflection to be such as to distinguish *Wetherellia* and *Palaeowetherellia* from Linaceae.

The true relationship of the fossils therefore remains to be discovered. They may belong to an extinct family whose nearest living allies have not yet been traced. But certain features point to Euphorbiaceae as a possible alliance. These features are the combination of loculicidal and septicidal dehiscence common in capsules of Euphorbiaceae, the number of radially arranged locules, and their tangential compression—such an arrangement is present in *Hura*—and the point of origin of the funicles from the axis which may be well below the apex of the fruit in many Euphorbiaceae. Pendulous seeds solitary in the locules with ventral raphe. At the same time it must be frankly admitted that no really comparable genus has yet been discovered, so that attribution to Euphorbiaceae must be regarded as doubtful. But no other known family shows so many of the characters of the fossil as the Euphorbiaceae.

## MATERIAL.

Fruit (Pl. 13, figs. 31–37). Also figured Kräusel (1939, pl. 2, figs. 9, 10 ; text-fig. 32). Neotype.

A nine-loculed fruit now fractured longitudinally to show one fertile and one abortive locule, the median axis and mode of placentation.

Cell patches of the inner carpellary layers adhere to the fertile locule-cast giving it a roughened granular appearance which at first sight simulates a rough testa (Pl. 13, figs. 33, 35). The elongate cells or striations of the locule surface are visible on the abortive locule-cast and the locule wall between it and the axis (Pl. 13, figs. 34, 36). The base of the specimen has decayed probably through long exposure before fossilization, displaying locules, locule-casts and seeds (Pl. 13, figs. 32–34). The carpel wall has also suffered from differential decay, which has produced deep superficial pits originally occupied by coarse-celled tissue especially on the lower surface (Pl. 13, fig. 32). Incipient loculicidal splitting is visible on one radial rib at the apex of the fruit (Pl. 13, fig. 31). Diameter, 19 mm. ; height, about 8 mm. (somewhat reduced by decay at the base).

From the Lower Danian (Upper Cretaceous) ; Farafra, Egypt. Brit. Mus. (N.H.), No. V.12985.

Part of a fruit (Pl. 13, fig. 38 ; Pl. 14, figs. 39–41).

A wedge-shaped loculicidal segment of a fruit bounded by the external surface on one side, and by two adjacent locules on its two lateral faces. The inner end of the wedge (fruit wall and axis) has broken or decayed, leaving exposed the locule and seed-casts projecting inwards (Pl. 14, fig. 40). Tangential breadth of segment, 6·5 mm. ; height, 7·5 mm. Radius from centre (as preserved) to outer edge, 7·5 mm. Estimated breadth of fruit, about 17 mm. Length of seed or locule-cast, 5·5 mm. ; breadth, 4 mm. ; thickness, 1 mm.

The exocarp is not preserved, the surface of the capsule is rough, not differentially decayed before fossilization as in V.12985. The substance is parenchyma with cells about 0·02 mm. in diameter in which patches of coarser parenchyma (cells about 0·05 mm. in diameter) are embedded. The decay of such coarse patches produced the deep pits in V.12985.

The locule-casts narrow to the exterior and are directly slightly upwards, at first sight suggesting parietal placentation. One was more fully displayed by removal of a few adherent fragments of the opposed carpel wall. Some of the parenchyma cells of the wall adhere at this narrow end of the locule-cast producing the effect of a rough nodular testa (Pl. 14, fig. 41).

Nearer the inner end of the locule abrasion has removed first the parenchymatous cells of the carpel and then a layer of locule-cast, thereby exposing the seed-cast (Pl. 14, fig. 41 *sc.*), with its angular equiaxial convex cell-impressions about 0·025 to 0·03 mm. in diameter (hence cells were concave inwards on the testa).

The testa is also represented by fragments of its external impression showing the same cell-impressions which are concave on this surface (hence the external surface had convex cells).

This fruit segment is clearly identical in character and size with Heer's figure of *Royena desertorum* (1876, pl. 1, figs. 11–16). But the details of its cell-structure and the arrangement of its locules also unite it with V.12985 and with another specimen figured in Pl. 14, figs. 42–47 ; Pl. 15, fig, 48. Hence this imperfect fruit constitutes a most important link in the evidence which unites *Royena desertorum* with *Palaeowetherellia schweinfurthi* (Heer).

From the Dano-Montian Lower Esna Shales ; Gebel Um-el-Ghanaim, Kharga Oasis, Egypt. Brit. Mus. (N.H.), No. V.31114.

A perfect six-carpelled endocarp (Pl. 12, figs. 24, 25) with base intact. The loculicidal sutures are clear, the septicidal more obscure except where abrasion has removed the outermost layers. The whole upper surface has been somewhat abraded showing the radiating groups of fine parenchyma. Diameter, 17 mm. ; length, 9·5 mm. Brit. Mus. (N.H.), No. V.31110.

A seven-partite endocarp, slightly asymmetrically developed. It is somewhat corroded on one side so that a seed (or locule-cast) is partially exposed. The exocarp is almost entirely abraded, one small patch only persisting at the base. The surface of the endocarp is also much abraded. The whole specimen is encrusted with mineral deposit which forms small pimples over the exposed fibre ends and coarse cell patches. Diameter, 17 mm. ; length, 10·5 mm. M. I. Youssef Collection, 1952.

Two segments of an endocarp showing the cavities of two locules. The lines of loculicidal dehiscence can be detected. The surface is somewhat abraded, exposing the irregular rugosities due to the radiating clusters of cells just below. A seed-cast in the locule between the two segments shows clear evidence of the ventral raphe. M. I. Youssef Collection, 1952.

The above three specimens are from the Dano-Montian Lower Esna Shales ; Gebel Atshan, Kosseir Area, Red Sea.

An eight-loculed endocarp (Pl. 12, fig. 26), perfect except for decay at the centre of the base so that the inner angles of the locules are exposed. The septa show median planes of weakness as for septicidal dehiscence. Five locules have retained their seeds, some of which are abortive; from the others the seeds have fallen through the gap caused by the decay above described. No exocarp is preserved, and there is considerable mineral incrustation over the surface of the abraded endocarp. Hollows for the fibre ends are visible on the lower surface; a few encrusted rounded knobs probably indicate their position on the upper surface.

Half of a fruit (Pl. 12, figs. 27, 28) which has been fractured longitudinally through two of the locules. One has a locule-cast preserved, in the other the locule-cast is missing, but the funicle (now much encrusted with a mineral deposit) is seen. There appears to be evidence of seven locules on this fragment, so that the complete fruit must have had at least eleven or twelve locules. Adherent remains of exocarp are seen at the base and apex only and are shown in section where the coat has broken away from the endocarp. Exocarp and endocarp are much encrusted by a mineral deposit. On the endocarp the encrusted remains of the fibres described on p. 170 form small rounded prominences.

Half of an endocarp which has split longitudinally (Pl. 12, figs. 29, 30). Three and a half carpels are preserved and the septicidal and loculicidal fracture lines are clearly visible.

The half carpel has split both loculicidally and septicidally and has been pushed out of position. The surface is sufficiently abraded to expose the radial grouping of the small cell-clusters. The network of fibres is obvious on one loculicidal suture plane, although owing to the adherent parenchyma and secondary incrustation the fibres are not themselves exposed but their position is very apparent. No exocarp is preserved. Diameter of endocarp, 18 mm.; length, 9 mm. A few small shell casts and impressions adhere to one fracture plane.

The above three specimens are from the Dano-Montian Lower Esna Shales; Abu Tundub, Kosseir Area, Red Sea. Brit. Mus. (N.H.), Nos. V.31111–13.

A fruit (Pl. 14, figs. 42–47; Pl. 15, fig. 48) with exocarp preserved but cracked in such a manner that at first sight it simulates three perianth segments (Pl. 14, fig. 42). Actual diameter (incomplete because the specimen had been polished on one side at *p* in figs. 42, 43 thus showing a tangential section), 18 × 17 mm. Estimated complete maximum diameter (distorted), about 24 × 17 mm. Height, 14 mm.

The whole fruit is cracked through desiccation and crushing, and is held together by calcite cement (white in the figures). On the polished surface two seeds can be seen, one in transverse and one in oblique section. The first shows the seed-cast (*sc*) surrounded fairly closely by the locule-cast (*lc*) (Pl. 15, fig. 48), which is embedded in the pulp or parenchyma of the carpel. The base of the fruit is sunk, and broken along one radius so that a beautiful seed-cast was exposed, at first held in place by calcite cement, but later becoming detached (Pl. 14, figs. 43–47). The beaked end of the compressed ovate cast was directed outwards and upwards in the locule as in the section of V.12985 shown in Pl. 13, figs. 33, 35, 37.

Length of seed-cast, 7 mm.; breadth, 4·75 mm.; thickness, 1·5 mm.

Surface of cast with equiaxial slightly convex cell-impressions. Their divergence at the beaked end indicates the micropyle. A shallow marginal furrow at the opposite rounded end of the cast dies out on the dorsal surface (close to an accidental fracture line). It indicates the inner end of the raphe, its termination marking the site of a small inconspicuous chalaza.

From the Dano-Montian Lower Esna Shales; Gebel Tarawan, Kharga Oasis, Egypt. Brit. Mus. (N.H.), No. V.31115.

Two segments of an endocarp showing the cavities of three locules. The carpel wall between the two segments is abraded so that the seed-cast is exposed along its dorsal margin. When the segments are separated the chalaza can be detected at the lowest point of the seed-cast as it lies in the endocarp.

The exterior of the endocarp is also abraded, so that in places the inner thick layer of fine parenchyma is exposed. Remains of the outer layer with radiating cell clusters occur in patches, but are much obscured by mineral incrustation. Length of endocarp, 8 mm.; maximum breadth across the two loculicidal segments, 14 mm.

From the Dano-Montian Lower Esna Shales; Gebel Durvi, Kosseir Area, Red Sea. M. I. Youssef Collection, 1952.

## Family ICACINACEAE

### Genus ***ICACINICARYA*** Reid & Chandler, 1933

### ***Icacinicarya youssefi*** n. sp.

(Pl. 15, figs. 49–51)

DIAGNOSIS. Fruit and endocarp almond-shaped or sub-obovoid in outline, lenticular in transverse section. External surface of endocarp with a series of more or less discontinuous irregular rugosities, some longitudinal, others transverse or oblique. Cells of endocarp markedly sinuous or coarsely digitate. Length of endocarp, 31 mm.; breadth, 22 mm.; thickness, 10 mm. Length of a fruit, 33 mm.; breadth, 26·5 mm.; thickness, 13 mm.

HOLOTYPE. Endocarp figured Pl. 15, fig. 51. Brit. Mus. (N.H.), No. V.31117.

LOCALITIES AND HORIZON. Gebel Atshan and Gebel Durvi, Kosseir Area, Red Sea; Dano-Montian Lower Esna Shales.

DESCRIPTION. *Fruit* (Pl. 15, figs. 49, 50): Bisymmetric, somewhat compressed, giving a lenticular transverse section, obovoid in outline, slightly mucronate at the apical style, attachment at the opposite extremity to the style. Surface much puckered as if by shrinkage of the mesocarp, but having a few rather ill-defined longitudinal ridges which may branch or anastomose halfway up. They may be due to fibres in the pulp or just beneath the epicarp. The actual epicarp itself is probably missing. One margin (overlying the funicle ?) thicker than the other with two or three marked longitudinal ridges. Whole surface with a pattern of small, rounded or quadrangular depressions, about 0·5 to 1 mm. in diameter, arranged in longitudinal rows. Finer structure of digitate or markedly sinuous cells. The convergence of the ornamentation at the two ends indicates the position of style and attachment described. Length of fruit, 33 mm.; breadth, 26·5 mm.; thickness, 13 mm.

*Endocarp* (Pl. 15, fig. 51): Similar in form to the fruit, base narrowed to a point where the opening for the funicle is clearly seen. A ridge due to splitting followed by mineral infiltration is seen at the apical style. This tendency to split at the stylar end has been observed in other Icacinaceae, e.g., *Natsiatum eocenicum* Chandler from the Lower Headon of Hordle.

As in genera of Icacinaceae one margin is much thicker and more rounded than the other. Experience has shown that the thick margin carries the funicle but no section is available, so this cannot be verified in the present instance. External surface with an obscure pattern of small mostly discontinuous rugosities, some elongate and longitudinally aligned. They do not produce a definite network of ridges and hollows as in *Icacinicarya platycarpa* Reid & Chandler (1933 : 345, pl. 16, figs. 11–18).

Surface of endocarp formed of small digitate or conspicuously sinuous cells with a tendency to transverse alignment. They are about 0·114 mm. broad and 0·057 mm. in length. Length of endocarp, 31 mm.; breadth, 22 mm.; thickness, 10 mm.

REMARKS AND AFFINITIES. Two specimens which by their general similarity may be presumed to belong to the same species although one shows the whole fruit, the other the endocarp only. One surface of the fruit shows the outline of a closely comparable endocarp owing to the contraction on drying which the pulpy exocarp has undergone (Pl. 15, fig. 50).

Although the most conclusive diagnostic characters of Icacinaceae can only be inferred because the unbroken character of the specimens conceals them, there can be little doubt of the relationship. The specimens are considerably larger than *Icacinicarya platycarpa*, which they resemble in their form, but as pointed out above, they can also be distinguished from that species by surface ornamentation. The cells of the endocarp are considerably larger than in that species and differ in their digitate form.

Although further information about this species is much to be desired, it is sufficiently well defined to be recognizable again, so that the specific name, *Icacinicarya youssefi*, after the finder, has been given.

### Family ICACINACEAE ?

### *ICACINICARYA* sp. ?

(Pl. 15, figs. 52–54)

LOCALITY AND HORIZON. Gebel Atshan, Kosseir Area, Red Sea; Dano-Montian Lower Esna Shales.

DESCRIPTION. *Fruit:* Sub-ovoid, bisymmetric about a plane which includes the two major axes and probably the funicle, although this was not actually seen, somewhat sharply angled in the plane of symmetry on one side, rounded and much inflated on the other (funicular margin). Style terminal at the apex, marked by a slight prominence. Attachment at the opposite end of the major axis to the style where the fruit shows a slight flattening, marked clearly by a small circular scar from which the surface cells radiate. The broad margin of the fruit is semicircular in outline ; the narrow margin is slightly concave immediately below the style and for about one-third of the length, but is convex for the lower two-thirds. Surface puckered and wrinkled giving a leathery appearance. Surface cells obscure except around the attachment where they are equiaxial, rounded, slightly convex, and about 0·038 mm. in diameter. Length of fruit, 13 mm. ; breadth in plane of symmetry, 11·5 mm. ; thickness at right angles to plane of symmetry, 11 mm.

REMARKS. The solitary specimen looks like a drupe with epicarp and mesocarp preserved so that all the characters of the endocarp are hidden except so far as they can be inferred from the form and symmetry of the specimen. The peculiar asymmetric outline as viewed at right angles to the plane of symmetry and the occurrence of one broad rounded and one angled margin may indicate a fruit of Icacinaceae. But pending the discovery of further evidence the specimen can only be referred tentatively to the form-genus *Icacinicarya.*

## Family FLACOURTIACEAE ?

## Genus ***THIEBAUDIA*** nov.

DIAGNOSIS. A large berry with about 36 parietal placentas, numerous seeds in two close set rows on the placentas, and a pulpy mass of tissue which occupies the whole of the fruit cavity. Seeds probably sub-ovoid. Length of fruit (compressed), 13 mm. ; breadth (much increased by compression but bereft of pericarp), 37 mm. Diameter of seeds, 1 to 1·5 mm.

TYPE SPECIES. *Thiebaudia rayaniensis* n. sp.

### ***Thiebaudia rayaniensis*** n. sp.

(Pl. 16, figs. 58–63)

DIAGNOSIS. As for genus.

HOLOTYPE. A single fruit with most of the pericarp removed. Thiébaud & Robson Collection (Locality no. 604), 1951. Brit. Mus. (N.H.), No. V.31120.

LOCALITY AND HORIZON. Wadi Rayan, Western desert of Egypt ; Eocene (? Lutetian or slightly younger).

DESCRIPTION. *Fruit :* A globular or sub-globular berry (now much compressed dorsiventrally, so that the wall has been buckled all around the equator of the specimen). Dehiscence probably by irregular breaking of the pericarp as no indication of sutures for regular dehiscence can be seen. The pericarp is preserved only at the extreme base and apex (Pl. 16, figs. 58, 59), elsewhere it has been broken away or abraded.

The external surface shows a few obscure radial flutings at the upper end, but is preserved in a matrix so coarse that it does not show the cell structure of the epicarp if still present.

A slightly defined and very slightly sunk area at the apex, about 5 mm. in diameter, may mark the base of the style. Thickness of pericarp about 3 mm. Numerous broad, rather flat, stout, longitudinal bands of fibres can be seen (although all are now incomplete) in the lower half of the fruit lying in fragmentary remains of the pericarp, but above the equator they appear to have been abraded. Placentation parietal, the seeds arranged in two close-set rows on each of thirty-six longitudinal placentas. Sometimes the seeds in the two rows are opposite one another, sometimes they appear to be alternate. Between each pair of placentas there is a very slight longitudinal ridge which thickens at its extreme apical end. These ridges produce on the inner surface of the pericarp a series of broad shallow longitudinal channels or pockets into which the placentas and seeds fitted.

Each placenta begins to produce its seeds at about 10 mm. from the apex of the fruit, where it springs from a pointed tongue of tissue with a narrow median furrow (Pl. 16, figs. 58, 60). The whole of the interior of the fruit is filled by a pulpy mass which adheres closely to the pericarp. The shallow ridges of the pericarp give rise to grooves upon the surface of the pulpy-mass. These separate the broad flat-topped ridges opposite the placentas bearing the concavities caused by the seeds.

It is the surface of this mass which is exposed intact on the upper surface of the specimen (Pl. 16, figs. 58, 60). The pulp is formed of coarsely and deeply sinuous cells, and throughout its thickness there are numerous small cavities about the same size as these cells (i.e., about 0·057 to 0·114 mm. in diameter.) No tendency to split either radially or otherwise has been detected in the pulpy mass.

Length of fruit (much reduced by dorsiventral compression), 13 mm.; breadth (correspondingly increased by compression but reduced by the loss of the pericarp), 37 mm.

*Seeds:* Very obscure. Producing sub-circular or sub-ovoid hollows on the pulpy mass (Pl. 16, figs. 58–61). Perhaps somewhat laterally compressed. The shallow convex external surface of the seed was ornamented with large inflated radially arranged cells or areoles diverging from a knob-like projection (Pl. 16, fig. 62). This structure is visible on the impression of a detached seed (probably belonging to the fruit) which is preserved on the pericarp near the base. Obscure traces of similar cells were also seen on a few seed-impressions on the pulpy mass. Other seed-impressions merely show a rounded prominence which must represent a considerable depression (hilar, micropylar, or chalazal ?) on the actual seed surface (Pl. 16, fig. 61, best shown in seed *s*). Internal casts of seeds (preserved in a few instances on the underside of the fruit but always incomplete, Pl. 16, fig. 63) show a smooth shining surface with longitudinal striations due to very long narrow cells with stout longitudinal walls, 0·014 to 0·018 mm. broad, lying parallel with the long axis of the seed. There are also slight traces of a coat of transversely aligned cells or fibres. Diameter of seeds, 1 to 1·5 mm. An internal cast measured 1·5 mm. in length, 1 mm. in breadth.

Remarks. One fruit preserved in a ferruginous cement filled with quartz grains forming a hard mass. It appears to have been embedded in a cream-coloured fine sand with Nummulites. The sand filled every crack and cranny of the cast, and a Nummulite (reported by Mr. C. D. Ovey as having a range from Lutetian to Middle Oligocene) was found in sand lying in the deep hollow between the lower surface of the pulpy mass and the remains of the pericarp at its base. There can be little doubt that the Nummulite belonged to the strata in which the fruit occurred, for little attempt had been made to clean the fossil of the adherent sand which clung with persistence. It has now been boiled and the sand brushed away. Other fossils from these beds are also said to be ferruginous, but this is the only plant as yet discovered. The age of the deposit is regarded as Lutetian, or possibly somewhat younger, but definitely Eocene.

As stated, most of the pericarp of this fruit was missing, revealing the central pulpy mass. It is a difficult specimen to understand and interpret. But probably, if its living counterpart were discovered, the description given above could be considerably simplified and shortened.

The coarseness of the matrix is not well calculated to preserve fine details. Little can be seen of the seed structure, especially as the hollows on the central mass are largely merely cavities in the pulp due to the pressure exercised by the growing seeds. They do not therefore give much information apart from the size and, rather obscurely, the form of the close-set seeds which are themselves almost entirely absent. Even these impressions are partially confused by some measure of overlap. The bases of the stout fibres in the fruit wall persist in broken ragged fragments at the base of the specimen, where they project from the fragment of pericarp. Sometimes they are missing, and the openings from which they came can be seen in the edge of the broken wall. The upper side of the specimen shows in good condition the surface of the pulpy mass with impressions made by the seeds on the ridges opposite the placentas, and the shallow furrows between these ridges which are the impressions of the narrow ridges on the pericarp wall described above.

The lower surface is less well preserved. It appears to have become torn and battered before or during fossilization, so that the actual lower surface of the pulpy mass together with the alignment and ridges on this surface is largely destroyed. Traces only of these features and of the collapsed and fragmentary pericarp wall with its fibres can be detected. Detached seeds represented by occasional external impressions or true internal casts have been pushed into the soft pulp and are visible here and there. Usually the casts are obscure. The true internal casts are rarer than the external impressions.

A curious and at first misleading feature of this specimen is a coarse transversely elongate meshwork of angular ridges around the equator. A radial fracture of the pulpy mass demonstrates the purely secondary and inorganic character of these ridges, which are due to the infiltration and setting of a limonite cement in cracks caused by buckling of the walls and pulp. No organic structure is to be seen in the seams of limonite which fill these cracks.

Affinities. The parietal placentation of this multi-carpelled fruit limits relationship to very few families. At first sight the specimen recalls a Poppy capsule on account of its radial symmetry and rounded small seeds, while the remains of the fruit wall at the apex simulate the stigma-bearing disc of *Papaver*. Here, however, the resemblance ends. The pulpy mass of the interior is wholly unlike anything in Papaveraceae. Parietal placentas associated with such a mass of pulp do, however, occur in Flacourtiaceae. But the difficulty here is that in no known genus of that family do as many as 36 placentas and carpels occur, while the details of seed structure in the fossil are too imperfectly known to be conclusive. No other living family appears to bear so close a relationship to this lovely fossil, and past experience has demonstrated the tendency for a larger number of locules to occur in fossil than in living forms, although not perhaps to the degree here recorded.

In the absence of more satisfactory information the specimen has been referred doubtfully to the family Flacourtiaceae. It has been given a new generic name, *Thiebaudia*, after one of the finders, while the specific name *rayaniensis* indicates the place where it was found.

The writer is of opinion that this specimen ought to be compared very carefully with Kräusel's species *Nymphaeopsis bachmanni* from the Lower Oligocene of Cairo. The supposed placenta and unequal hammer-shaped involucral segments of that species may quite possibly be parts of a pericarp which has cracked and contracted into irregular segments on drying. Such a feature is displayed by one fruit of *Palaeowetherellia* from Kharga (Pl. 14, fig. 42), in which the cracked berry with its mineral infiltrations simulates a trifid perianth. The fibres shown by Kräusel (1939, pl. 2, figs. 2, 3, 6) on the surface exposed beneath the supposed involucral segments are not altogether unlike those of *Thiebaudia*. The direction in which they branch suggests that the supposed apex is in fact the base of the specimen. The buckling of the fruit at the equator due to dorsiventral compression has produced a similar network of infiltration ridges to those described in *Thiebaudia*. It is not impossible that the apparent operculum of the seeds might be interpreted as a large chalazal scar. But these are merely suggestions for future consideration. They cannot be substantiated without the most careful study of the specimens themselves.

### *Carpolithus hassani* n. sp.

(Pl. 16, figs. 64, 65)

LOCALITY AND HORIZON. Gebel-el-Ter, Kharga Oasis, Egypt; Dano-Montian Lower Esna Shales.

A beautiful but puzzling specimen suggests one valve of a bisymmetric endocarp. It appears to have been rubbed down artificially at the margins but to no great depth. The outline, as it exists at present, is broadly elliptical, 20 mm. long, 17·5 mm. broad, 5·5 mm. deep. The external surface is gently convex and the internal correspondingly concave. The thickness of the wall at the polished margin is 2 to 2·5 mm.

Three deep external grooves must have some structural significance. They appear to be the outer edges of slits which pass through the whole thickness of the wall. The two nearest the margins of the valve slope inwards towards the centre of the fruit so that their inner edges, marked by deep grooves on the surface of the locule, lie slightly closer together than do their outer edges on the external surface of the valve. These two grooves are parallel with the outline of the valve, but they do not meet, although their ends lie much closer together at one extremity (apex ?) of the valve than at the other. One groove is longer than the other. The third groove which pierces the endocarp also, lies midway between the other two but is shorter than either. It begins at about the middle of the valve and passes towards that end of it (base ?), where the other two grooves are most widely separated. It dies out before reaching the edge of the valve. Within the slits the surface of the endocarp is longitudinally striate.

On the exterior, between the longer curved marginal groove and the short median one, a longitudinal slightly sinuous furrow can be seen which was evidently a channel for a fibre, impressions of which are seen. It gives off two or three short slender branches at its upper end. These diverge and taper upwards.

Surface of valve rough, due to the convex angular walls of the parenchymatous cells of which it is composed. Cells 0·05 to 0·1 mm. in diameter. Locule surface smoother, formed of equally large equiaxial cells.

A first glance at this specimen suggests that it may belong to Menispermaceae. But closer scrutiny shows that the relationship is impossible for the following reasons :

(1) The curved marginal grooves do not unite at the apex to form a horseshoe, nor does one of their opposite ends curve appreciably outwards.

(2) The external grooves correspond with internal grooves and not with internal ridges as in Menispermaceae, where the ridges form a cavity for the curved seed.

(3) The endocarp of Menispermaceae is fibrous in structure, not parenchymatous.

I have found no fruit with such peculiar slits which may be connected with germination. Possibly the curved area enclosed by the slits may be associated with a curved embryo.

### ***Carpolithus*** sp. (***Icacinicarya*** sp. ?)

(Pl. 16, fig. 66)

LOCALITY AND HORIZON. Gebel-el-Ter, Kharga Oasis, Egypt ; Dano-Montian Lower Esna Shales.

The internal cast of a valve of an endocarp 10·5 mm. long, 9·25 mm. broad, 1·8 mm. deep. The cast is formed of coarse crystalline ferruginous matter. Its surface shows an obscure network of ridges. The internal surface of the actual specimen would have shown corresponding grooves separated by shallow convexities. No cell-structure is visible. The form of the valve suggests Icacinaceae, but the evidence preserved is insufficient for certainty.

### ***Carpolithus*** sp.

(Pl. 16, figs. 55–57)

LOCALITY AND HORIZON. Gebel Atshan, Kosseir Area, Red Sea ; Dano-Montian Lower Esna Shales.

A sub-globular fruit slightly laterally compressed, with a three-angled apex, the angles meeting in a slight prominence. They die out at about the middle of the fruit. Between these well-marked angles a few subsidiary inconspicuous longitudinal ridges can be seen. Basal attachment small, slightly sunk, marked by a little projection at the middle of the hollow. At the extreme base of the fruit there are three short, very shallow, rounded furrows opposite the three apical ridges or angles. Surface, as now preserved, ornamented with numerous angular, more or less equiaxial contiguous concave areas, somewhat variable in size, up to 1 or 1·5 mm. in diameter but sometimes smaller. This cast is formed of radiating groups of fine cells, the groups often but not invariably coinciding with the concavities. Length of fruit, 13·5 mm.; diameter, 10 by 13·5 mm.

There is nothing to indicate the identity of this specimen.

## APPENDIX I

### NOTE ON THE OCCURRENCE OF THE FOSSIL FRUITS AND SEEDS COLLECTED FROM THE KHARGA OASIS, WESTERN DESERT OF EGYPT

By M. Youssef Hassan

The specimens were collected from a bed with an average thickness of 35 metres. It is composed of dark grey and greenish shales, well foliated and often densely seamed with gypsiferous and salt intercalations. Red nodules of botryoidal limonite, sometimes attaining large sizes, are abundant. Frequently the limonite appears in pseudocrystalline form, being cubes sometimes with interpenetration twinning. The bed is rich in fossils which are dwarfed and excellently preserved in limonite. The age of this bed is " Danian " or more probably Dano-Montian. The following is a complete list of the fossil fauna identified:

*Schizorhabdus libycus* Zittel.<br>
*Palaeopsammia multiformis* Wanner.<br>
*Bathypsammia cleopatrae* Hassan MS.<br>
*Trochocyathus epicharis* Wanner.<br>
*Trochocyathus deniseptatus* Hassan MS.<br>
*Dungulia libyca* (Wanner).<br>
*Pattalophyllia aegyptiaca* (Wanner).<br>
*Terebratulina* sp.<br>
*Pentacrinus* sp.<br>
*Nucula tremolate-striata* Wanner.<br>
*Nucula chargensis* Quaas.<br>
*Leda leia* Wanner.<br>
*Trapezium* sp.<br>
*Trapezium* aff. *acutangulum* (Deshayes).<br>
*Cardium* cf. *becksi* Muller.<br>
*Cardium* cf. *inaequiconvexum* Cossman & Pissarro.<br>
*Crassatella zitteli* Wanner.<br>
*Cucullaea schweinfurthi* Quaas.<br>
*Cucullaea* sp.<br>
*Limea* sp.<br>
*Chlamys mayer-eymari* (Newton).<br>
*Verticordia nova* Hassan MS.<br>
*Corbula striatuloides* Forbes.<br>
*Trochus* cf. *laryi* D'Archiac & Haime.<br>
*Scala calamistrata* (Wanner).<br>
*Architectonica dachelensis* (Wanner).<br>
*Natica* (*Gyrodes*) *farafrensis* Wanner.<br>
*Natica* (*Euspira*) *terensis* Hassan MS.<br>
*Rissoa* cf. *crassistriata* Wood.<br>
*Campanile* cf. *brookmani* Cox.<br>
*Cerithium abictiforme* Wanner.<br>
*Cerithium bigeniculatum* Wanner.<br>
*Cerithium* cf. *periphractum* Wanner.<br>
" *Alaria* " *schweinfurthi* Quaas.<br>
*Cypraea* cf. *kayei* Forbes.<br>
*Tonna* sp.<br>
*Tudicla peroni* Quaas.<br>
*Sassia tuberculosa* (Kaunnowen).<br>
*Sassia farafrensis* (Quass).<br>
*Sassia chalmasi* (Quaas).<br>
*Sassia* sp.<br>
*Athleta* (*Volutilithes*) *daniensis* (Quaas).<br>
*Cyclichna* cf. *regulbiensis* (Adams).<br>
*Solidula chargensis* (Quaas).<br>
*Solidula pharaonum* (Wanner).<br>
*Avellana cretacea* Quaas.<br>
*Pygopolon* sp.<br>
*Nautilus applanatus* Wanner, *ex* Zittel MS.<br>
*Nautilus desertorum* Quaas, *ex* Zittel MS.

This horizon is resting on a series of alternating marls and impure limestones with occasional phosphatic bands of undoubtedly late Maestrichtian age.

## APPENDIX II

### NOTE ON THE OCCURRENCE OF THE FOSSIL FRUITS AND SEEDS COLLECTED FROM THE KOSSEIR AREA (RED SEA), EGYPT

By Murad I. Youssef

The fruits were collected from a single bed in different localities in the Kosseir Area (Red Sea). The bed in which these fossil fruits, as well as the fossils mentioned below, were found is a greyish-green shale varying in thickness between 50 and 125 metres. The concretions found throughout this bed, and the fossils occurring generally in a band near its middle part, are all limonitic. Cubic pseudomorphs of limonite, probably after pyrite, are also found. Irregular gypsum veins running in every direction, perhaps corresponding to the more or less pyramidal planes of jointing of the shales, are epigenetic, being secondary in origin.

The fossils collected from this bed are considered to be Danian or Dano-Montian. Some 30 metres of shales and marls lying immediately below this bed are of the same age. These are underlain by Maestrichtian rocks containing many phosphate and phosphatic beds.

The following is a list of the fossil fauna identified from the thick shale bed :

*Brachycyathus daniensis* Wanner.
*Trochocyathus epicharis* Wanner.
*Pattalophyllia aegyptiaca* (Wanner).
*Caryosmilia granosa* Wanner.
*Dungulia milneri* (Gregory).
*Dungulia libyca* (Wanner).
*Caryophyllia jasmundi* Wanner.
*Palaeopsammia multiformis* Wanner.
*Stephanophyllia* (*Microbacia*) sp.
*Serpula* cf. *discoidea* Wanner.
*Pentacrinus* sp.
*Salenia* sp.
*Cyphosoma* sp.
*Hemiaster chargensis* Wanner.
*Hemiaster* (*Leucaster*) *lamberti* Cottreau.
*Terebratulina chrysalis* (Schlotheim).
*Terebratulina* sp.
*Nucula chargensis* Quaas.
*Nucula lucida* J. Boehm.
*Nucula tenera* J. Müller (*non* S. V. Wood).
*Nucula tremolate-striata* Wanner.
*Leda leia* Wanner.
*Thyasira cretacea* (Wanner).
*Cardium* cf. *inaequiconvexum* Cossmann & Pissarro.
*Cardium* cf. *becksi* Müller.
*Trapezium* sp.
*Lucina dachelensis* Wanner.
*Crassatella matercula* Mayer-Eymar.
*Arca modioloides* Wanner.
*Cucullaea* sp.
*Chlamys mayer-eymari* (Newton).
*Verticordia nova* Hassan MS.
*Scala* cf. *desertorum* Wanner.
*Natica farafrensis* Wanner.
*Campanile* cf. *brookmani* Cox.
*Alaria schweinfurthi* Quaas.
*Alaria* sp.
*Sassia chalmasi* (Quas).
*Neptunea zitteli* (Quaas).
*Neptunea* sp.
*Fusus* sp.
*Athleta* (*Volutilithes*) *desertorum* (Quaas).
*Solidula chargensis* (Quaas).
*Avellana cretacea* Quaas.
*Avellana* sp.
*Cylichna* cf. *regulbiensis* (Adams).
*Dentalium bicarinatum* Wanner.
*Nautilus desertorum* Quaas, *ex* Zittel MS.

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NOTE.—While this paper was going through the press my attention was drawn to a memoir by L. W. LeRoy (Biostratigraphy of the Maqfi Section, Egypt. *Mem. Geol. Soc. Amer.*, Washington, **54**, 1953) in which, from a study of the Foraminifera, the author concludes not only that the "Esna Shales" are definitely Lower Eocene, but also that the Danian is probably unrepresented in Egypt. There may, however, be some unresolved confusion over the use of the term "Lower Esna Shales."

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## PLATE 10

### *Nipa burtini* (Brongniart)

Fig. 1. The domed apical end of a drupe which is incomplete below the middle. Length preserved, 25 mm.; breadth, 27 mm. Estimated complete length, about 45–50 mm. It shows the typical longitudinal fibro-vascular bundles embedded in parenchyma. (*u*) the apical umbo. × 2·8. (V.31105.)

Fig. 2. The same, viewed from below, looking on to the fractured surface. The side shown in fig. 1 is towards the top of the figure. Part of the unridged smooth endocarp (*e*) is exposed. Transverse fibres of the endocarp are obscurely seen. The pericarp is in section at (*p*, *p*) and in surface view with its longitudinal fibres at (*f*). × 2·8.

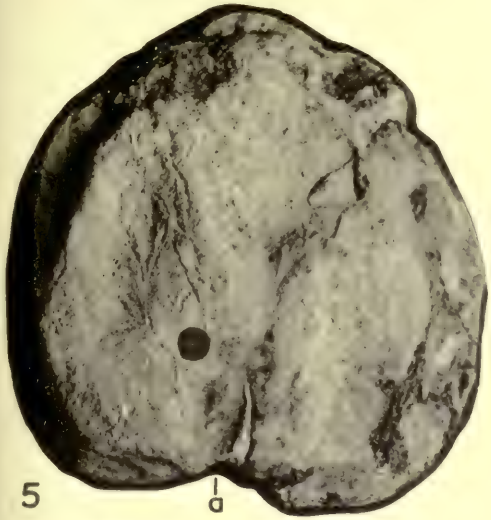
Fig. 3. An obliquely distorted seed-cast in which the basal aperture (*a*) occupies a basi-lateral position. Slight longitudinal flutings of the surface are visible. There is a mosaic pattern all over the surface. × ½ approx. (V.13239.)

Fig. 4. The opposite surface of the same seed-cast, apical end, showing the sub-apical funnel-shaped opening (*ch*) and the raphe-fibre impressions converging towards it and passing into it. (*m*) marks the apical mucro of the nut. × 1·2.

Fig. 5. A seed-cast so compressed as to be almost lenticular. (*a*) is the position of the basal aperture. The coarse network of fibres which lay between the two integuments of the testa is faintly impressed upon the cast to the left of the median line. × ½ approx. (V.13240.)

### *Nipa fruticans* Thunberg

Fig. 6. A seed for comparison with fig. 5 from which the outer coat of the testa has been entirely removed. Most of the inner coat has also been removed except beneath the slightly sunk coarse network of fibres (*f*, *f*) which lay between the two coats and which still adheres to the seed. In the meshes between the fibres (where the inner coat has gone) the transverse alignment of the small ruminations of the endosperm can be seen rather obscurely. The seed has been cut longitudinally. × 2 approx. Recent; Singapore.



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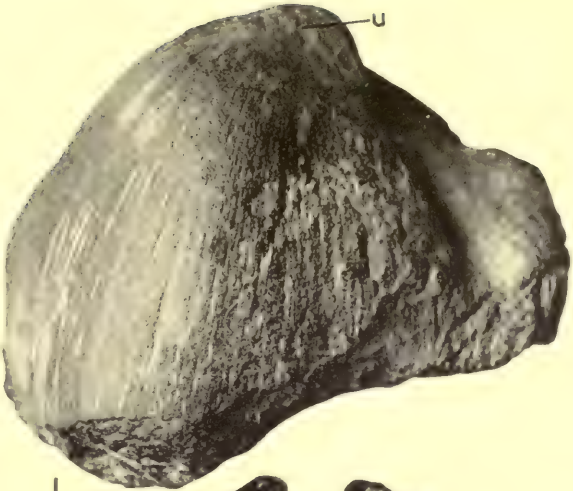

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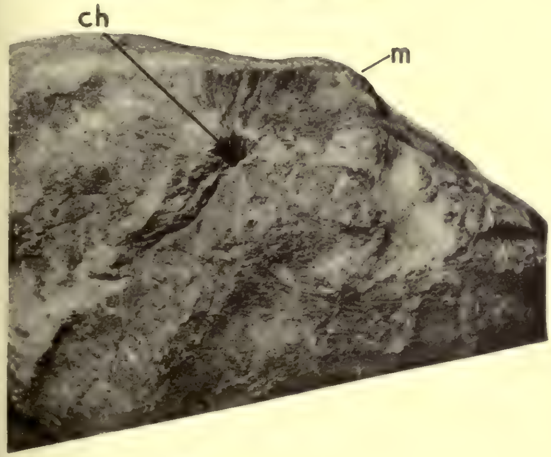

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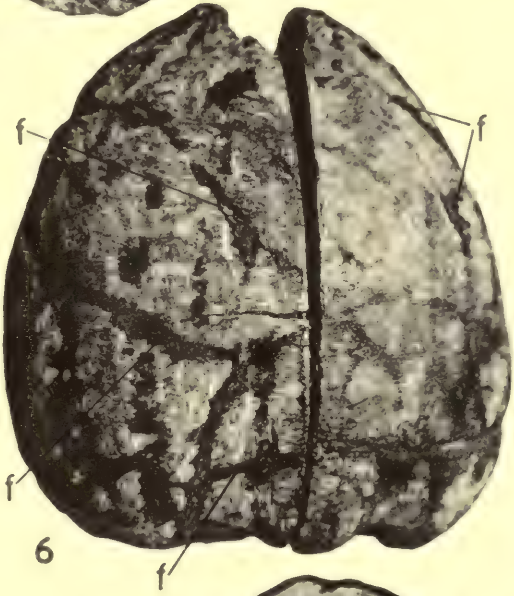

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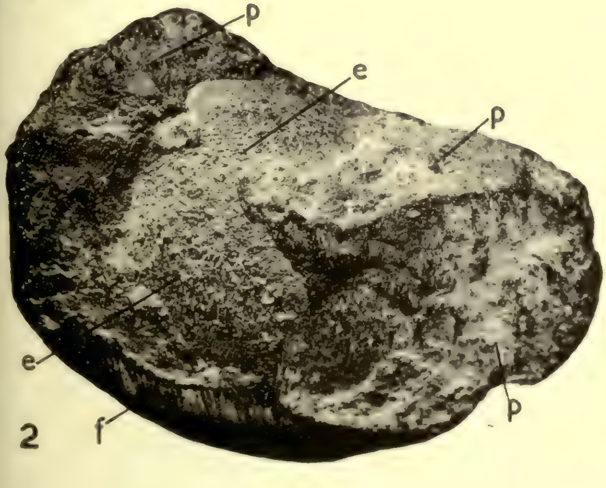

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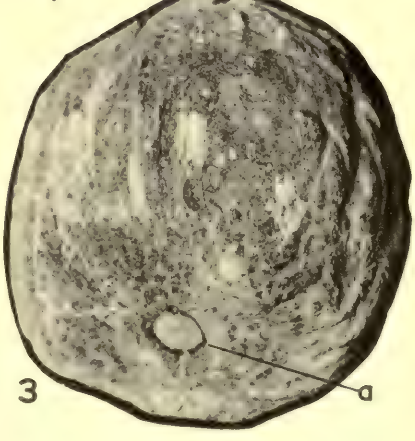

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NIPA BURTINI, NIPA FRUTICANS

## PLATE 11

### *Nipa burtini* (Brongniart)

FIG. 7. Opposite side of the seed-cast in Pl. 10, fig. 5, showing detail of endosperm structure. The elongate alignment at (*r*) indicates the position of the raphe, the radial arrangement indicates the point of entry of the raphe fibres (*ch*) below the apex of the cast. × 1·8.

FIG. 8 The same seed-cast, detail of the surface depicted in Pl. 10, fig. 5, showing the more normal transverse alignment of the endosperm. × 1·8.

FIG. 9. The base of a seed with its ribbed outer integument partially preserved but sufficiently abraded to expose the flat broad fibre band (*f*). The basal aperture is clearly seen. The specimen has undergone much lateral compression. × 1. Figured by Kräusel, 1939, pl. 1, fig. 24 as *Rubiaceocarpum markgrafi*.

### *Nipa fruticans* Thunberg

FIG. 10. A seed, side, showing the ribbed outer integument with clear impressions of the longitudinal, and more obscure impressions of the transverse, endocarp fibres. × 1·7. Recent; Singapore.

FIG. 11. The seed in Pl. 10, fig. 6, showing the flat raphe band (*r*) lying in a shallow longitudinal furrow of the endosperm. On each side of the band the transverse alignment of the endosperm is visible. Above where the band has been removed irregular arrangement of the endosperm is exposed at (*ch*) and just below longitudinal alignment can be detected. × 2 approx.

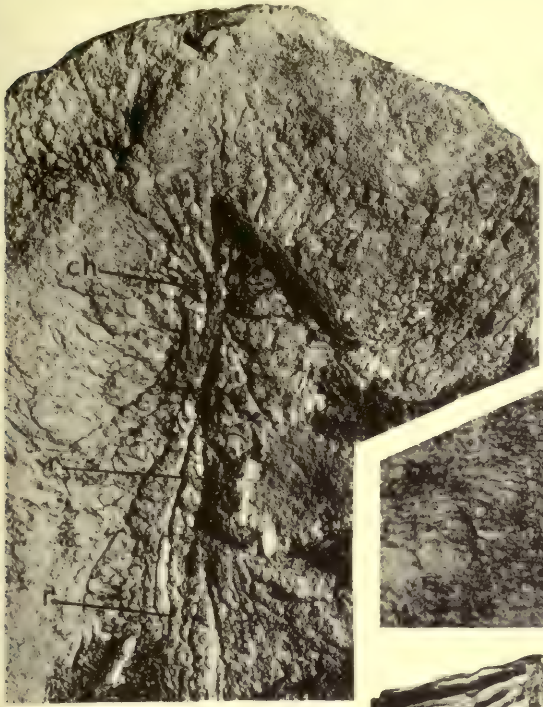
FIG. 12. The same seed, base, showing the aperture for the radicle, the deep furrow (*g*) due to the incomplete septum which projected from the locule-wall, and shallow furrows or sinuosities of the surface. The raphe lay in the furrow at (*r*). × 1·75.

### *Anonaspermum aegypticum* n. sp.

FIG. 13. The distal end of a seed-cast showing typical ruminate endosperm with encircling raphe seen at (*r*, *r*). The fibrous remains of testa still adhere in the depression at the middle of the broad surface. The specimen had been fractured transversely and the hilar end was missing. (*ch*) indicates the beginning of the chalaza, most of which has been broken away with the hilar end. × 3. (V.31106.)

FIG. 14. The same, end view. It shows the encircling raphe partly broken on the left so that the ruminations are exposed in section at *rs*. The çhalaza begins at (*ch*). × 3.

FIG. 15. The same, fractured surface, showing the four-partite endosperm. × 3.



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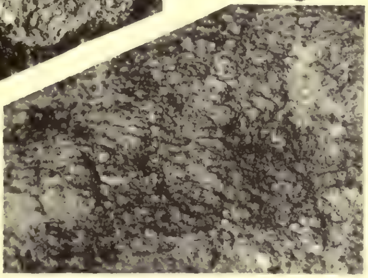

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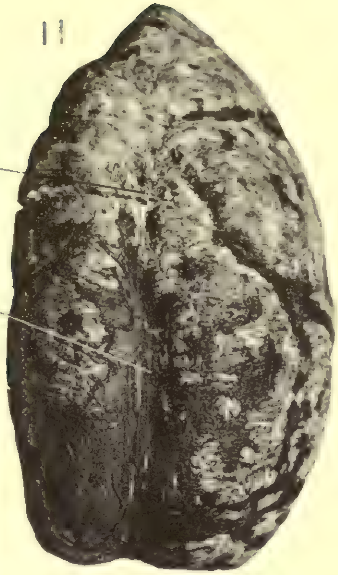

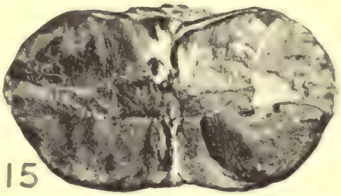

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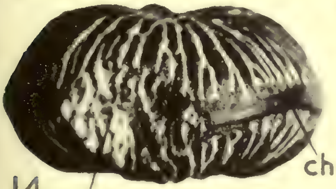

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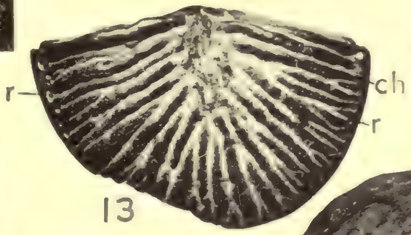

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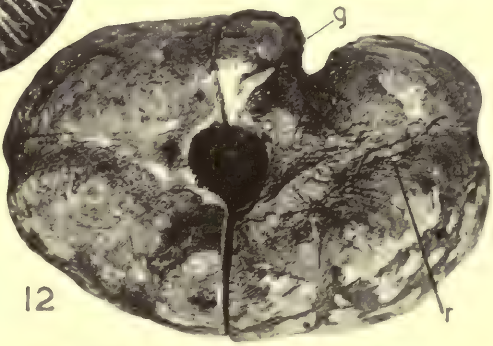

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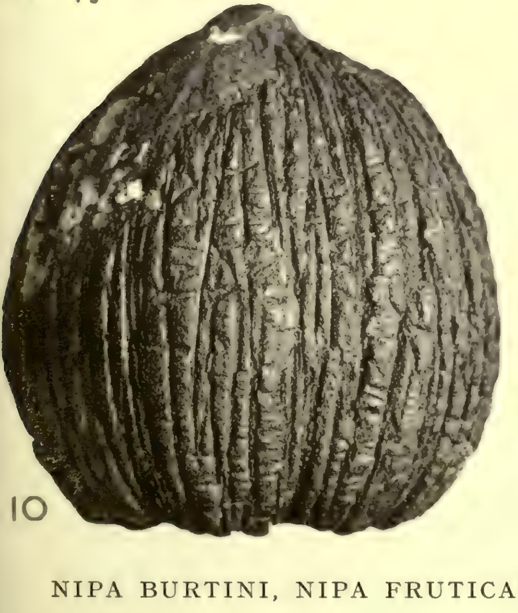

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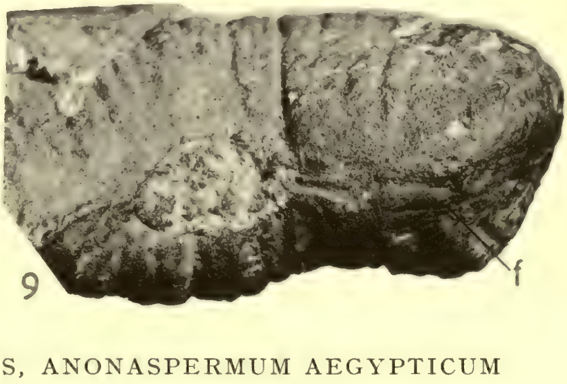

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NIPA BURTINI, NIPA FRUTICANS, ANONASPERMUM AEGYPTICUM

## PLATE 12

### *Lagenoidea trilocularis* Reid & Chandler

FIG. 16. Side view of a fruit showing three of the six loculicidal segments of the capsule. × 3. (V.31107.)

FIG. 17. Base of the same specimen, showing the attachment scar and wrinkled epicarp which partially obscures the segments. × 3.

Fig. 18. Apex of the same, showing more clearly the six segments and lines of dehiscence. × 3.

FIG. 19. Side view of a second specimen showing three segments clearly; the edge of a fourth is just visible on the right-hand margin of the figure. × 2·8. (V.31108.)

FIG. 20. The same, base, showing six segments and an aperture where placenta and perianth have broken away. × 2·6.

### *Lagenoidea bilocularis* Reid & Chandler

FIG. 21. A fruit, side, showing the narrow median segment representing the edge of the septum, and two of the broader lateral segments. × 3. (V.31109.)

FIG. 22. The same, apex, showing the narrow median segments which form the ends of the septum and the two pairs of segments which overlie the locules. Loculicidal splitting occurs at (*l*, *l*), septicidal splitting at (*s*, *s*). × 3.

FIG. 23. The same, base. The septum is damaged on one side at this end of the fruit. Lettering as in fig. 22. × 3.

### *Palaeowetherellia schweinfurthi* (Heer) Chandler

FIG. 24. Lower surface of a six-carpelled endocarp showing the six loculicidal suture lines (*l*, *l*). Slight abrasion of this surface has displayed the radiating groups of fine parenchyma which produce a pitted effect. Decay at the centre of the base has scarcely started. × 2·8. (V.31110.)

FIG. 25. The same, apex. The outer part of the carpel wall is corroded in places showing the finer-celled parenchyma of the layers beneath. Loculicidal sutures are clear; the septicidal ones (*sp*, *sp*) between them are more obscure except where abrasion has partly removed the outer layers of the endocarp. × 2·8.

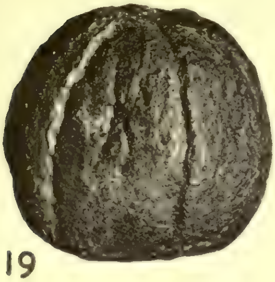
FIG. 26. The under surface of an eight-loculed endocarp, perfect except for the characteristic decay at the centre of the base so that locules and septa (showing planes of weakness associated with septicidal splitting) are exposed. Several locules have shed their seeds. In others the seeds are ill-developed. × 2·8. (V.31111.)

FIG. 27. The base of half a fruit which retains a considerable patch of exocarp (*ex*) over the median area. Around the circumference the exocarp has been worn away exposing six segments of endocarp representing seven locules (*l*, *l*). × 2·8. (V.31112.)

FIG. 28. The fractured surface of the same showing two locules. The one on the right is occupied by a locule- and seed-cast. (*ch*) indicates the position of the chalaza. The left-hand locule is empty but the much encrusted funicle (*f*) is visible. Its origin in the axis is obscured by mineral deposit. (*ex*) = exocarp in section. × 3.

FIG. 29. Base of another incomplete endocarp with three and a half segments representing four locules (*l*, *l*). The half segment on the right has slipped out of position along the loculicidal fracture plane (*l*). The surface of this half segment shows the plane of septicidal fracture (*sp*). × 2·8. (V.31113.)

FIG. 30. The same, looking on to the fractured surface. (*sp*) is the septicidal fracture plane. (*l*, *l*) indicates loculicidal surfaces. The network of fibres is seen on the right-hand loculicidal suture surface. The left locule surface is obscured by molluscan casts (out of focus in the figure). × 3.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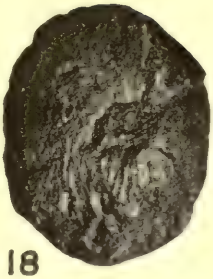
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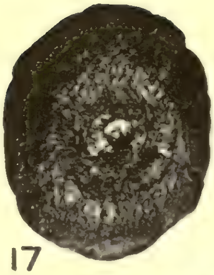
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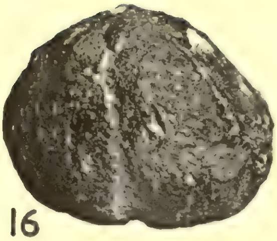
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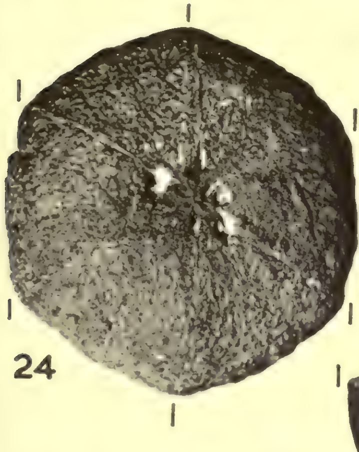

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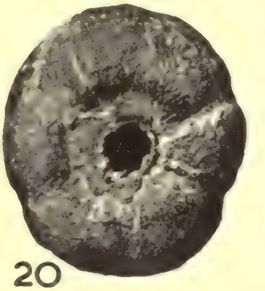
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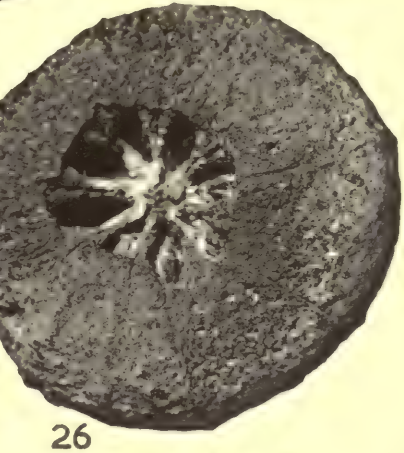
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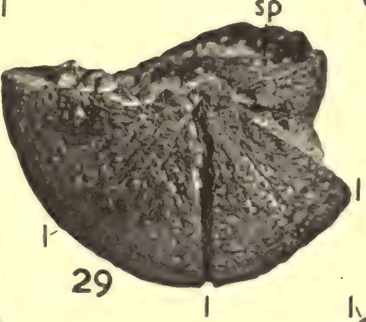

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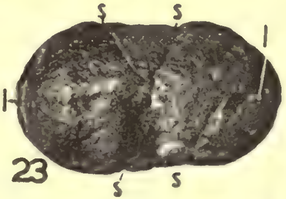

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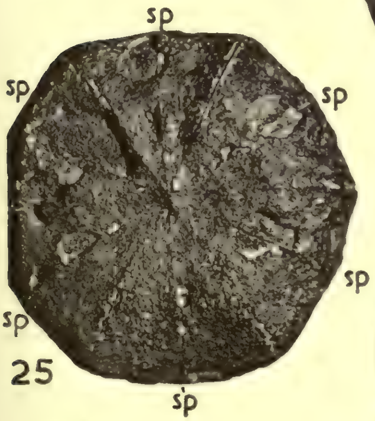
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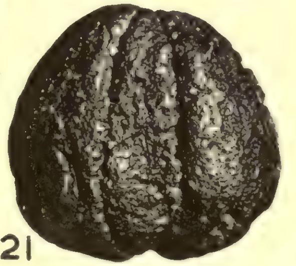
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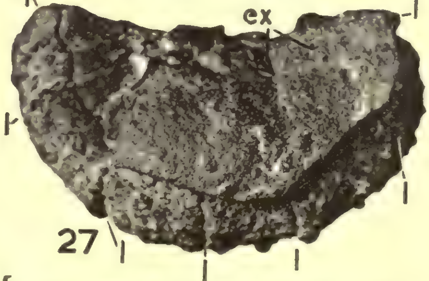

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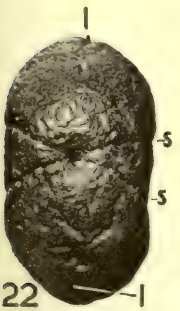

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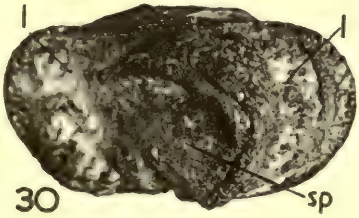

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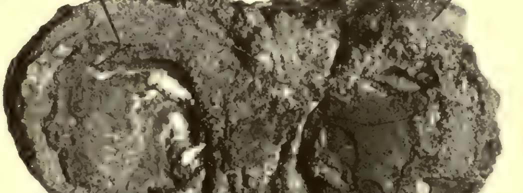

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LAGENOIDEA TRILOCULARIS, L. BILOCULARIS, PALAEOWETHERELLIA SCHWEINFURTHI

# PLATE 13

## *Palaeowetherellia schweinfurthi* (Heer) Chandler

FIG. 31. The apex of a nine-carpelled fruit polished by abrasion. (*l*, *l*) indicates planes of loculicidal dehiscence. Between them, but more obscure, are radial lines indicating planes of septicidal dehiscence (*sp*). At (*ls*) incipient loculicidal splitting can be seen at the middle of the ridge. The specimen has been fractured along the line (*f*, *f*). The small circular scar at the centre may be the axis or the style base. × 3. (V.12985.)

FIG. 32. The same, base, corroded at the centre so that the locules are exposed (some now empty). Note the conspicuous pits over the surface due to the decay of fibres surrounded by coarse parenchymatous patches. Lettering as in fig. 31. × 3.

FIG. 33. The fractured surface (longitudinal section) of the above showing a locule-cast on the left with the funicle arising from the axis of the fruit and passing in the plane of the locule to the hilum situated near the upper outer angle. The right-hand locule is empty. × 3.

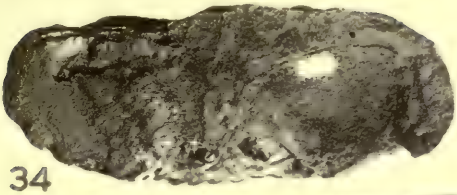
FIG. 34. The counterpart half of the same, showing on the right the locule surface which overlay the cast in fig. 33, and on the left an abortive locule-cast which occupied the empty locule in fig. 33. × 3.

FIG. 35. The left-hand part of the section in fig. 33. A larger magnification shows the funicle just above the locule-cast and the entry of the funicle into the cast marking the position of the hilum on the enclosed seed. This fertile locule lies at (*fl*) on the left of fig. 32 where the edge of the cast is seen. Around the hilar end of the cast adherent patches of tissue torn from the endocarp simulate a rugose testa. × 7.

FIG. 36. The left-hand part of the section in fig. 34. The fibres of the axis show more clearly. Oblique fine striations on the surface of the abortive locule close to the axis are visible and the small abortive locule-cast is shown at (*a*). This locule lies at (*fl*) on the left of fig. 31. × 7.

FIG. 37. The same as fig. 34, right-hand side of specimen, with a detached seed from another specimen laid in the locule to show the approximate position that the seed would have occupied. Axial fibres (*a*) and funicle (*f*) are well shown in the endocarp wall and on the flat surface of the locule respectively. The curved line at the rounded end of the seed is an accidental fracture. × 7. (cf. Pl. 14, figs. 43–47.)

FIG. 38. A segment of another fruit which has broken loculicidally, apex. Axis to left at (*a*), circumference to right, loculicidal surfaces above and below. × 6. (V. 31114.)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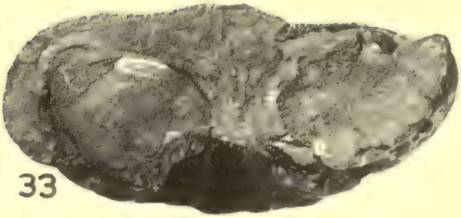
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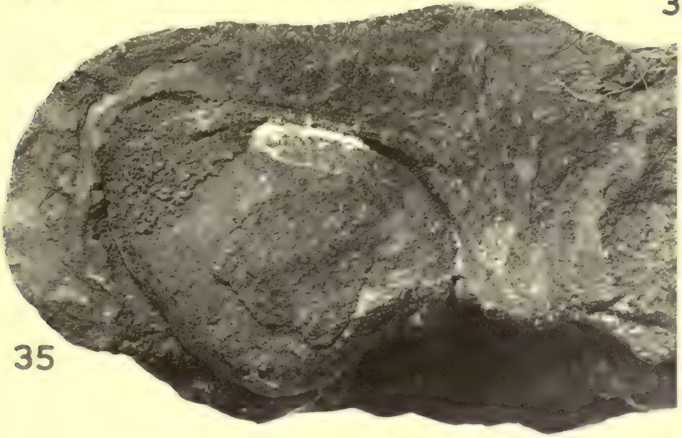
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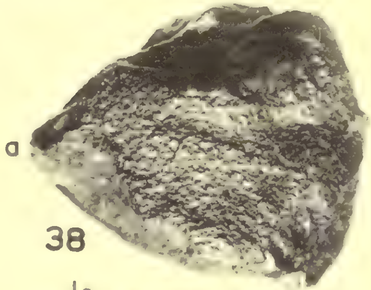

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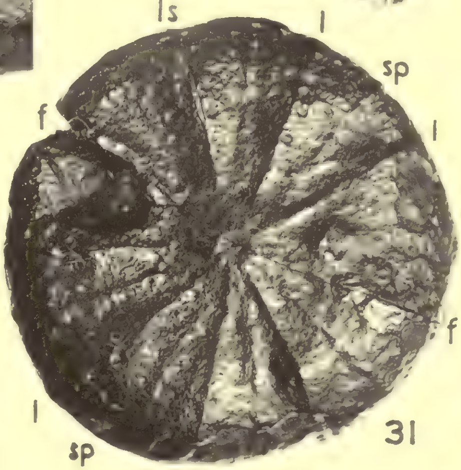
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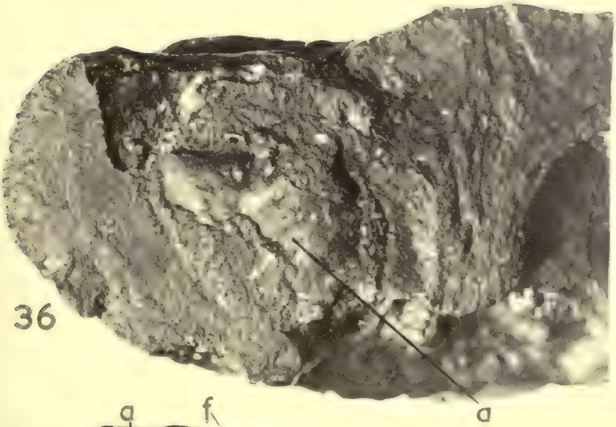

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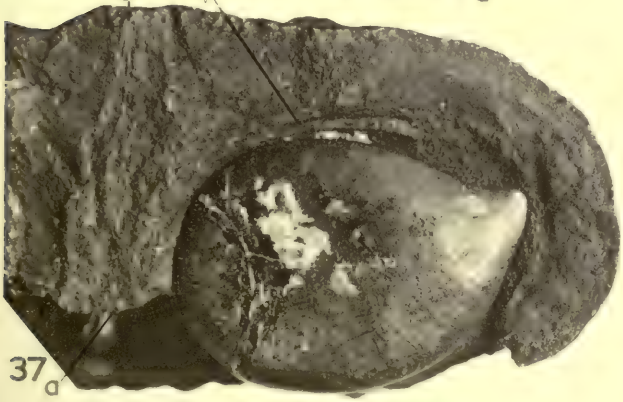

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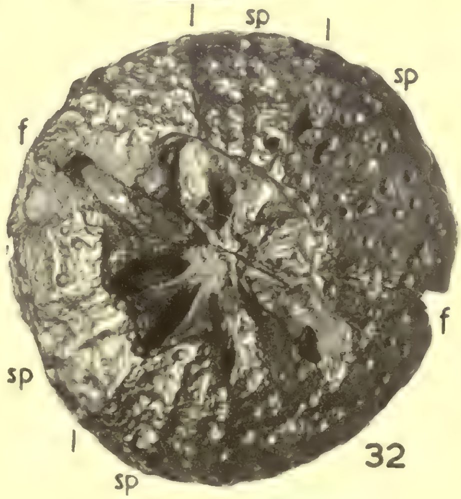
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PALAEOWETHERELLIA SCHWEINFURTHI

## PLATE 14

### *Palaeowetherellia schweinfurthi* (Heer) Chandler

Fig. 39. Side view of the fruit segment in Pl. 13, fig. 38. It shows the rounded inner end of a seed-cast (*c*) exposed by the breaking away in fossilization of the axis and inner angle of the carpel. Specimens with similar proportions were separated by Heer (1876) under the name *Royena desertorum*. × 6.

Fig. 40. The same, looking on to the inner edge where the two locules and seed-casts can be seen. × 6.

Fig. 41. Opposite side of the segment to that shown in Fig. 39. Part of the carpel wall still adheres to the cast at the outer end ; it conceals the hilar end of the seed and embracing locule-cast, and produces the false effect of a rough nodular testa. The smooth surface at (*lc*) is the remains of the thin locule-cast closely adherent to the seed. To the left at (*sc*) the film of locule-cast has broken away, exposing the seed-cast. A narrow band of the smoothly finished loculicidal surface is preserved at (*ls*), but elsewhere this surface has been torn away, thereby exposing the angular cells of the carpel wall at (*cw*). × 10.

Fig. 42. Apex of another fruit (incomplete as indicated by dotted lines) with exocarp preserved. Crushing and drying have caused the specimen to crack, white calcite has been deposited in the cracks which give a false appearance of three perianth segments. The specimen had been rubbed down along a plane parallel with its axis at (*p*). × 1·8. (V.31115.)

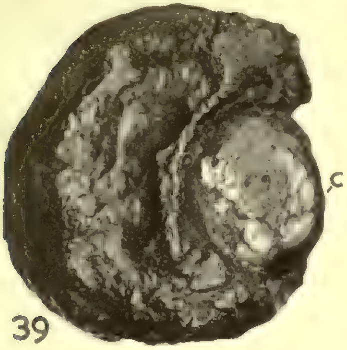
Fig. 43. The same, base. A crack on the right exposes a shining seed-cast. This cast is illustrated laid in the locule of another fruit in Pl. 13, fig. 37. Calcite-filled cracks are again seen. Lettering as in fig. 42. × 1·8.

Fig. 44. Part of the same, more highly magnified and tilted to show the seed-cast of which the lower margin is exposed. × 6.

Fig. 45. The same seed-cast, removed from the fruit, showing the narrow ventral edge. The micropyle is at (*m*), the hilum at (*h*). The plasticene in which it was necessary to mount the specimen to obtain this view of the seed somewhat obscures its outline at the lower end of the figure. × 6·5.

Fig. 46. The same seed-cast, side view. (*m*) indicates the position of micropyle and radicle, (*h*) that of the hilum. The chalaza lay near the lower end of the accidental fracture line. × 10.

Fig. 47. The same cast, opposite surface, to show the bisymmetry of the seed. × 10.



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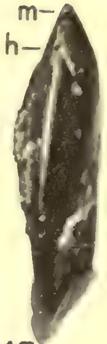

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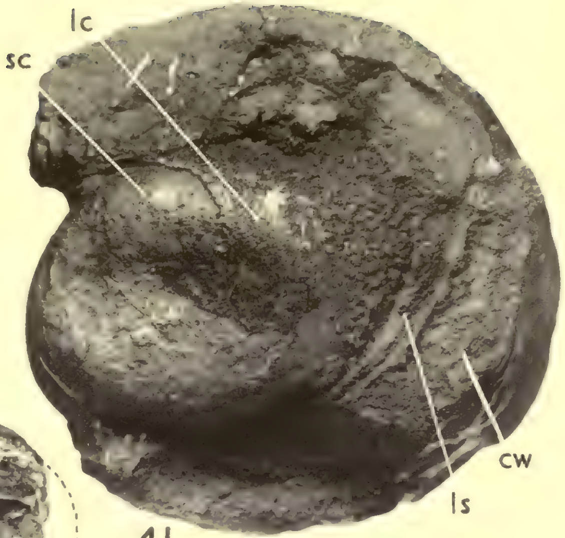

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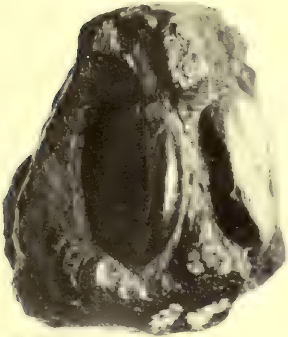

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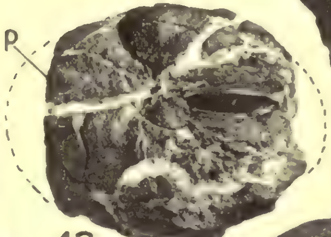

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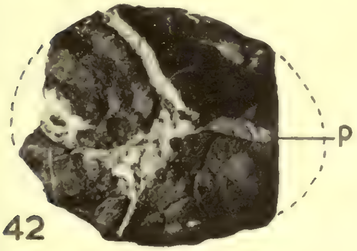

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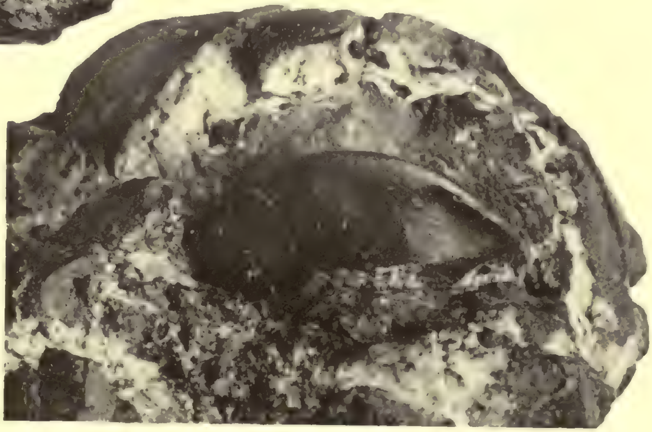

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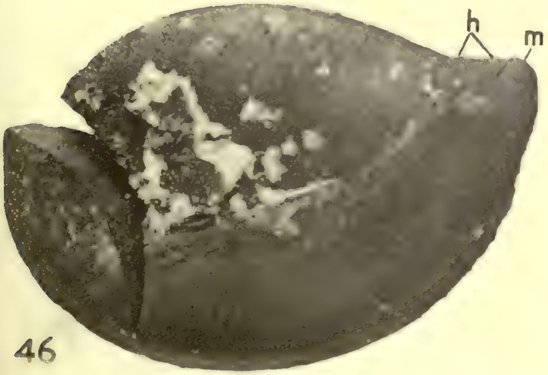

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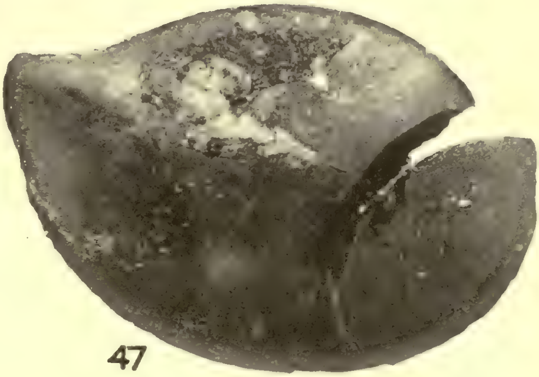

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PALAEOWETHERELLIA SCHWEINFURTHI

## PLATE 15

### *Palaeowetherellia schweinfurthi* (Heer) Chandler

FIG. 48. The partially polished surface (*p*) of the fruit in Pl. 12, figs. 41, 42, showing a tangential section through a locule and seed. The seed-cast (*sc*) is closely embraced by the locule-cast (*lc*) lying between the two thick loculicidal valves of the carpel. The raphe (*r*) is probably indicated by the slightly constricted area at the narrow upper edge of the seed-cast. The white mass to the right is calcite filling the loculicidal split and now cementing together the two valves of the carpel (*v*, *v*). × 10.

### *Icacinicarya youssefi* n. sp.

FIG. 49. A fruit, broad surface, showing form and ornamentation. (*st*) indicates the position of the style. The funicle was situated in the right margin of the enclosed endocarp. × 2·6. (V.31116.)

FIG. 50. The same, opposite surface. Contraction of the pericarp has brought out the outline of the endocarp within. × 2·6.

FIG. 51. An endocarp bereft of the pericarp. Note the surface ornamentation, the basal aperture for the entry of the funicle at (*f*), and the short vertical fracture with infiltrated mineral substance at the stylar end (*st*). × 2·6. (V.31117).

### *Icacinicarya* sp. ?

FIG. 52. Side view of a wrinkled drupe showing the asymmetry characteristic of Icacinaceae. The more convex left margin may be presumed to carry the funicle. (*st*) indicates the style. × 2·8. (V.31118.)

FIG. 53. Base of the same, showing the inflated funicular margin (below) and narrow opposite margin (at the top of the figure). The small circular scar of attachment, from which the cells radiate, is seen at the centre. × 3.

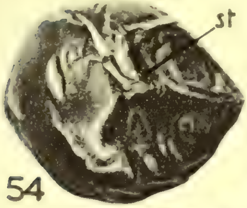
FIG. 54. Apex of the same. Funicle bearing margin to the left. Style at (*st*). × 2·6.

### *Carpolithus* sp.

FIG. 55. Fruit, side, showing an angle at the apical end and small angular concavities all over the surface. × 2·8. (V.31119.)

FIG. 56. The same, apex, showing the three angles or ridges and the surface concavities. × 2·6.

FIG. 57. The same, base, showing the slightly sunk attachment and the surface concavities, as well as the shallow grooves which lie opposite the apical angles. × 3.



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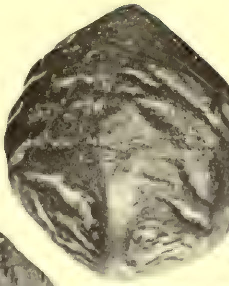

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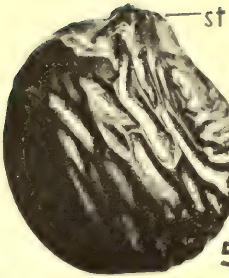

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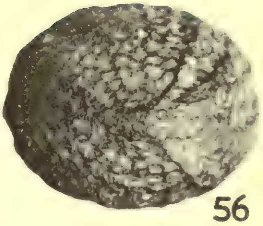

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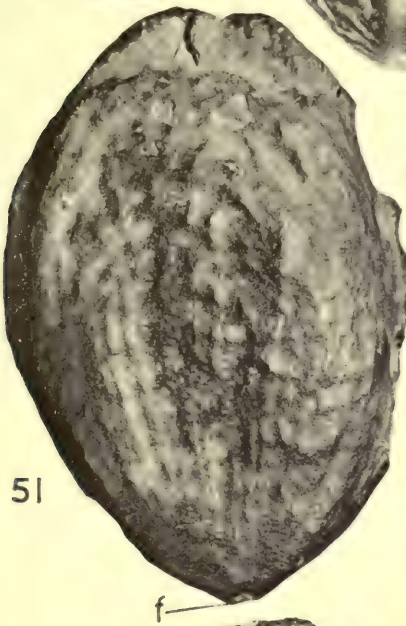

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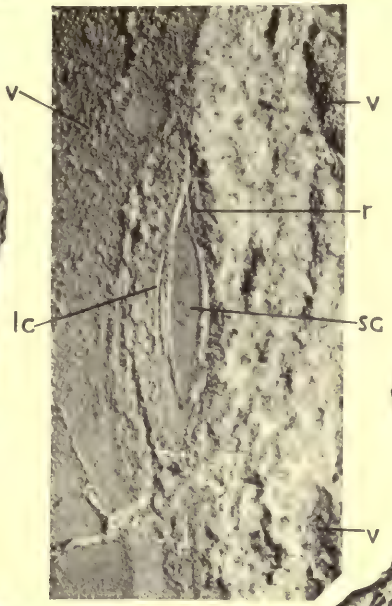

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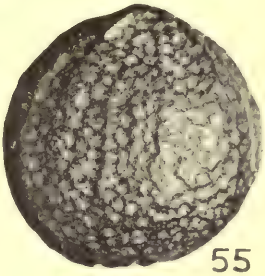

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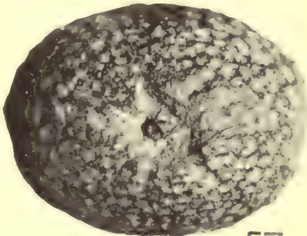

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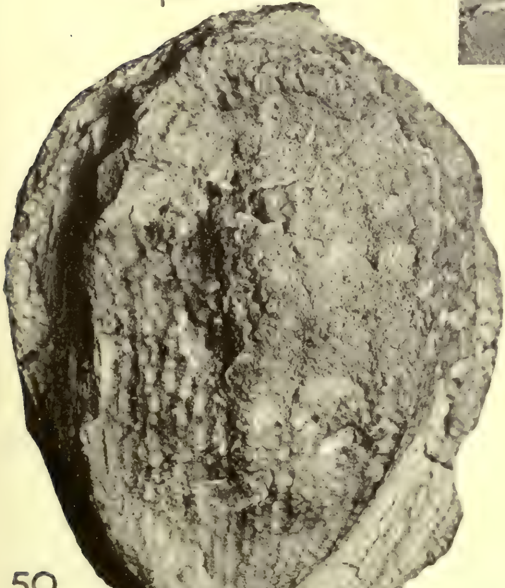

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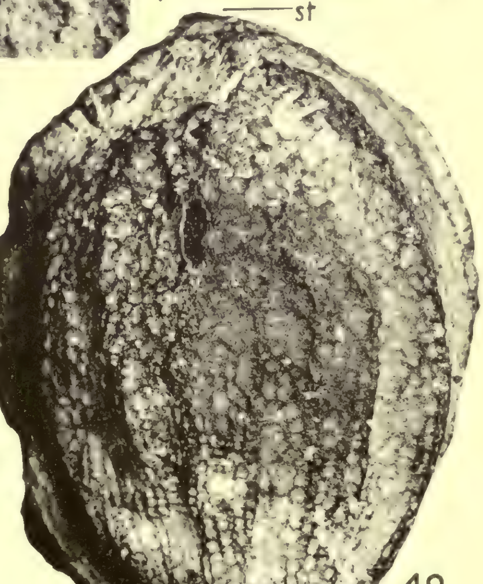

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PALAEOWETHERELLIA SCHWEINFURTHI, ICACINICARYA YOUSSEFI, ICACINICARYA SP. ? CARPOLITHUS SP.

## PLATE 16

### *Thiebaudia rayaniensis* n. gen. et sp.

FIG. 58. Apex of fruit. The pericarp is preserved only at the centre. It shows shallow, inconspicuous, radial furrows diverging from a slightly sunk circular area (perhaps the style base). Where the pericarp is broken away, the pulpy mass which fills the fruit cavity is exposed. On the surface of this mass radial furrows mark the position of shallow longitudinal ridges which must have projected from the fruit-wall. Between them impressions of the placentae are seen each with two rows of seeds now represented by the hollows which they produced on the surface of the pulp. Each placenta arises from a short tongue of tissue with longitudinal median furrow. These tongues project from beneath the edge of the remaining pericarp. × 1·6. (V.31120.)

FIG. 59. The same, from below. Here the pericarp is preserved only at the very centre of the base. The radial furrows (so clear on the upper surface) are obscure, for this surface has been much battered and partially destroyed. The arrangement of the seeds has been disturbed, but a few external seed impressions and internal casts are preserved scattered somewhat irregularly. A small concavity, seen at the lower edge of the central fragment of the pericarp, may be the external impression of a detached seed (cf. fig. 62). × 1·6.

FIG. 60. Part of the upper surface (indicated by (*x*) in fig. 58). It shows more clearly the seed pockets on each side of the placentas, and the impressions of the ridges described above. The margin of the fragment of pericarp lies near the base of the figure at (*p*). × 6.

FIG. 61. Part of the under surface (indicated by (*x*) in fig. 59) showing a few of the hollow pockets for the seeds. They sometimes show a central projection (best seen in the hollow marked *s*) which suggests a concavity on the surface of the seed. A few broken fibre-fragments (remains of pericarp) adhere to the pulpy mass. × 6.

FIG. 62. The external impression of the seed (?) on the pericarp in fig. 59 as described above. The surface of the pericarp was painted white around the impression to bring out its outline. A central depression must correspond with a prominence on the seed itself. Coarse cells or areoles are obscurely seen diverging from this central depression. × 16.

FIG. 63. A somewhat imperfect internal cast of a seed from the lower surface of the pulpy mass. Striae due to cells on the surface of the cast lie parallel with its longer axis. Although the cast is obscure a sharp marginal angle suggests a bisymmetric form. × 20. (V.31120.)

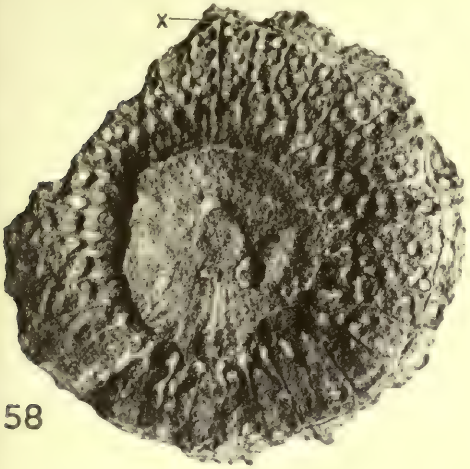
### *Carpolithus hassani* n. sp.

FIG. 64. The exterior of a valve showing three deep furrows and a branching fibre which is partially embedded in the surface between the right-hand furrow and the short middle one. × 1·8. (V.31121.)

FIG. 65. The internal aspect of the same, showing that the wall is pierced by the three external furrows. The thickness of the wall is also shown. The smooth marginal areas appear to have been artificially produced by polishing. × 1·8.

### *Carpolithus* sp. (*Icacinicarya* sp. ?)

FIG. 66. The internal cast of a valve of a fruit showing form and ornamentation suggestive of Icacinaceae. × 1·8. (V.31122.)



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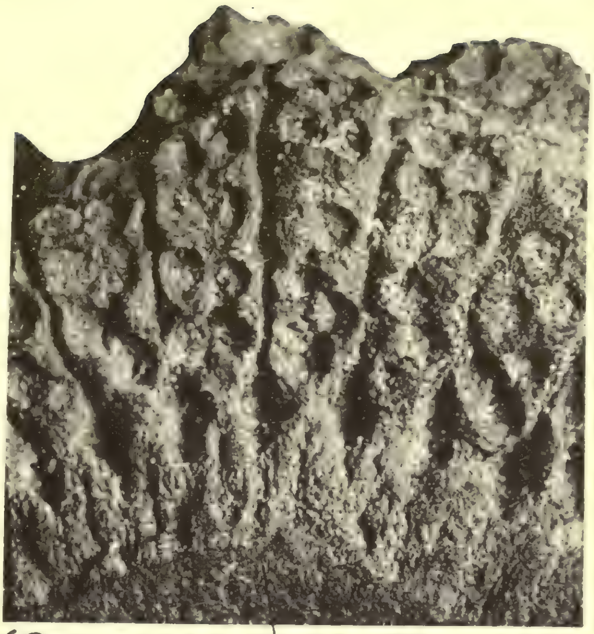

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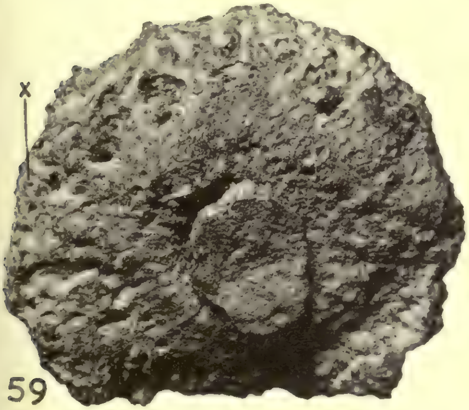

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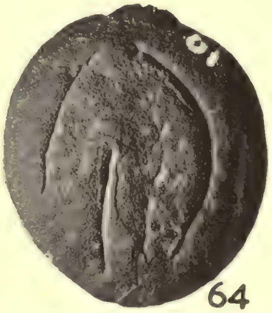

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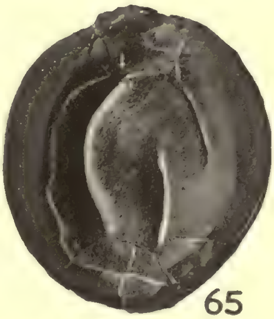

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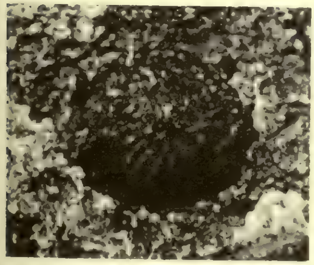

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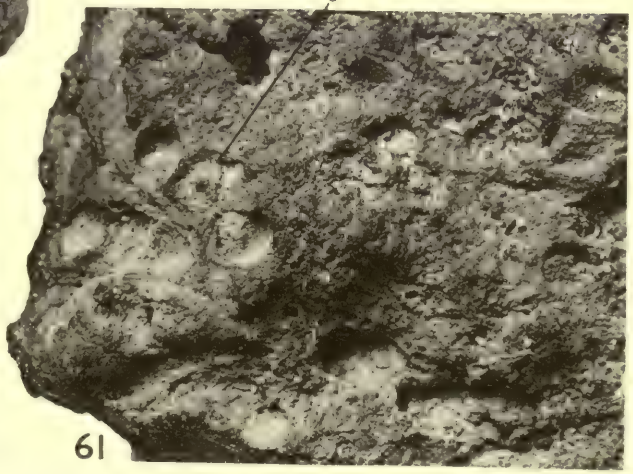

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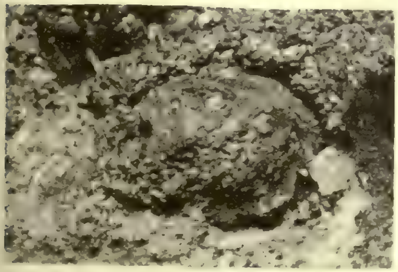

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THIEBAUDIA RAYANIENSIS, CARPOLITHUS HASSANI
CARPOLITHUS SP. (ICACINICARYA SP. ?)

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# THE CARBONIFEROUS FLORA OF PERU

W. J. JONGMANS

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 2 No. 5
LONDON: 1954

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# THE CARBONIFEROUS FLORA OF PERU

BY

WILHELMUS JOSEPHUS JONGMANS

*Pp.* 189–224 ; *Pls.* 17–26

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# THE CARBONIFEROUS FLORA OF PERU

*By* W. J. JONGMANS

## SYNOPSIS

A reconsideration of all the older records of Carboniferous plants from Peru, together with an examination of two important newer collections, fully confirms the Lower Carboniferous age of the flora. Several new species are described, including representatives of *Lepidodendropsis*, and the world distribution of this genus is reviewed.

## INTRODUCTION

THE Carboniferous flora of Peru has been the subject of several papers. The principal flora is found on the peninsula of Paracas, which, as Berry (1922) points out, is largely made up of continental Carboniferous sediments and constitutes one of the very few deposits of this character in South America, and the only known occurrence of rocks of this age on the west coast of South America. Somewhat to the north-east of the peninsula there are other Carboniferous localities at Huanuco and in the neighbourhood of Cerro de Pasco. Up to the present little has been known of the flora of these localities. Gothan (1928) mentions *Rhacopteris circularis* Walton from Vichaicoto and S. Huanuco and *Knorria* and a *Calamites*-like specimen from Cachama, between Cerro de Pasco and Huanuco. Fortunately one of my former assistants, Dr. N. de Voogd, sent me a good collection from Carhuamayo. This collection and another from Paracas, put at my disposal by the Trustees of the British Museum, will be described in this paper.

## REVIEW OF THE LITERATURE ON THE CARBONIFEROUS FLORA OF PERU

Almost at the same time as Berry, Seward (1922) described another set of plants from Paracas. According to these papers the outcrop at Paracas was first discovered by Fuchs (1900). Seward states: "The coal occurs in a series of greenish sandstones and grey and black carbonaceous shales, which have a north-easterly strike and dip about 25° south-eastwards. These are overlain unconformably on the neck of the peninsula by Tertiary sandstones and impure limestones. There is no definite stratigraphical evidence of the age of the coal-bearing beds, and the plants are therefore of special importance."

Fuchs (1900) recorded the following species: *Calamites suckowi* Bgt., *Sphenopteris hartlebeni* Dkr., *Baiera pluripartita* Schl., *Lepidodendron sternbergii* Bgt., *Sigillaria tessellata* Bgt., and *Stigmaria ficoides* Bgt.

Fuchs assigned the beds to the Upper Coal Measures, but his list is scarcely possible ; it contains common Carboniferous plants and Wealden species.

The Carboniferous flora was mentioned subsequently by Fuchs (1905), Dorca (1909), Marsters (1909) and Lisson (1917), without any reference to the Wealden species. Lisson's paper is the only one which contains any new facts on this flora ; he mentions *Lepidodendron rimosum* and *L. obovatum*, determined by Zeiller. The age is given as Westphalian. Some critical remarks will be given when treating the papers by Berry (1922) and Gothan (1928).

The next contribution to the Carboniferous flora of Peru was that by Steinmann (1911) who did not visit Paracas. He examined Fuchs' collection at the Cuerpo de Ingenieros de Minas in Lima, and listed the following forms for the Paracas flora : *Archaeocalamites radiatus*, *Lepidodendron* cf. *veltheimi*, *L.* cf. *volkmanni*, *Sphenopteris affinis* (*furcata*), *Rhodea filifera* and *Rhabdocarpus*.

The occurrence of these species would prove that the flora belongs to the Lower Carboniferous. It is interesting but somewhat remarkable that the plant-bearing Carboniferous should be of Lower Carboniferous age and the invertebrate-bearing Carboniferous of Upper Carboniferous age. Unfortunately no literature on the invertebrate fauna of the Peruvian Carboniferous is known to me, and so far as can be seen from the sections in Berry's papers (1922, 1922*a*) no invertebrate fauna had been met with on the peninsula of Paracas during his visit. Steinmann states that no marine fossils are known from Paracas. He visited a second Carboniferous locality near Huichaycota, some kilometres south of Huanuco on the Huallaga and found large stems of *Lepidodendron* and at different places many specimens which he records as *Rhacopteris inaequilatera* Goepp.

The introductory paper by Berry (1922*a*) contains no descriptions of the plants, but discusses the locality and the history of the knowledge of the flora up to that date and records the following :

*Palmatopteris furcata* (Bgt.), *Eremopteris whitei* Berry, *E. peruianus* Berry, *Calamites suckowi* Bgt., *Calamostachys* sp., *Lepidodendron rimosum* Sternb., *L. obovatum* Sternb., *Lepidophyllum* sp., *Lepidostrobus* sp., *Stigmaria* sp. and *Knorria* sp.

Berry visited Paracas and was able to make large collections ; his remarks on the locality and the mode of occurrence of the plants are very valuable. According to Berry the fossil plants occur at different horizons in the sections he examined, and " there is no chronologic change in the flora from top to bottom although fossil plants are more varied in the lowermost horizon. The materials are relatively coarse throughout and would seem to indicate rapid deposition." Over half of the section " is described as sandstone, which is often coarse and arkosic. Of the 273 feet described as shale 192 feet are distinctly sandy, so that less than 14% of the total thickness [of 585 feet], including the so-called coal seams, is fine-grained shale and even the coal contains much silty impurities. No underclays with rootlets, or upright stems were observed and the coaly layers have every appearance of having been formed of drift material " (Berry, 1922*a* : 191–192).

The flora is " extremely limited, although some of the elements are exceedingly common," especially the plants recorded as *Palmatopteris furcata*, *Eremopteris whitei*, *Calamites suckowi* and *Lepidodendron rimosum* (Berry, 1922*a* : 193). Berry imagines " that the coarseness of the sediments and the apparent drifting of the material are mainly responsible for the absence of a more representative flora." Thus his collections contained " no traces of *Sigillaria, Cordaites, Sphenophyllum, Calamite* foliage, nor of any Neuropterids, Pecopterids, Alethopterids or Lonchopterids." He states that this feature of the flora is undoubtedly responsible for Steinmann's opinion (1911) that the Paracas flora is of Lower Carboniferous age. According to Berry the Paracas Carboniferous corresponds to the Westphalian stage.

In the same year Seward (1922) described a collection of plants from Paracas made by J. A. Douglas in 1911. Seward's flora contains *Sphenopteris* sp., *Lepidodendron* sp., *Sigillaria* (or *Lepidodendron*) sp., *Bothrodendron* sp., and Planta incertae sedis. His determinations are considered in detail below:

*Sphenopteris* sp. (Seward, 1922, pl. 13, figs. 1–3) is present in several fragments. " The branched axis is longitudinally striated and smooth; the pinnules are more or less deltoid, deeply dissected, and the ultimate segments are obtuse or truncate." Seward compares it with *Sphenopteris furcata* Bgt., but in this species the segments are acute. He also compares it with *Eremopteris missouriensis* Lesquereux (White, 1899, pl. 5, figs. 1–3*a*) which does possess obtuse or truncate ultimate segments.

Several Lower Carboniferous species have pinnules which closely resemble the Peruvian specimens; " the deeply dissected form of the lamina suggests comparison with pinnules of *Rhodea* and *Sphenopteridium*." Thus Nathorst (1920, pl. 1, figs. 11–13) figures as *Sphenopteridium norbergii* a plant which he compares with *Sphenopteris affinis* L. & H.; the latter differs in its broader, thicker segments, and its stronger and more numerous nerves. It will later be shown that such comparison is important for the determination of the specimens and their age.

*Lepidodendron* sp. (Seward, 1922, pl. 13, figs. 4–6). The most important specimen (fig. 4) shows a branch with attached leaves. It is preserved on a carbonaceous sandstone and most of the details cannot be seen. However, it is clear that the " cushions " of the leaves are separated by undulate lines, that succeeding " cushions" are connected at the upper and lower ends, and that the surface is striated, though not in the deeply impressed portions of the cushions. Seward's fig. 5 shows some details on the leaf-cushion and the leaf-scar.

On pl. 13, fig. 6 Seward figures a *Lepidodendron* which he considers belongs to the same species as those illustrated in figs. 4, 5. The specimen is interesting as it shows the leaf-like organs very clearly. It somewhat resembles the figure published by Johnson (1913, pl. 41, fig. 3), but it is impossible to decide whether it is a portion of a cone or not. The long erect leaves are narrow and possess a distinct middle nerve. They are sharply pointed at their ends.

*Sigillaria* (or *Lepidodendron*) sp. (Seward, 1922, pl. 13, figs. 7, 8). " Pieces of a stem having contiguous leaf-cushions which bear leaf-scars agreeing both with some types of *Sigillaria* (e.g., *S. brardi* Bgt.) and with certain species of *Lepidodendron*. On the upper part of several leaf-cushions there is a small circular scar, presumably a ligule-pit. No vascular bundle scars or parichnos-scars can be detected." Seward compares his specimens with those named *S. brardi* from South Africa (Seward, 1897: 326) and Brazil (White, 1908), which, however, probably do not belong to Brnogniart's species, nor even to the genus *Sigillaria*. He also compares them with *S. mutans* Weiss & Sterzel (1893 : 84). It is very curious that Seward should compare his specimens with a true Stephanian species.

*Bothrodendron* (?) sp. (Seward, 1922, pl. 13, fig. 9 ; text-fig.). Seward describes two specimens under this heading " although it is by no means certain that the specimens shown in pl. xiii, fig. 9, and in the text-figure belong to the same species."

The specimen figured in pl. 13 shows " spirally-disposed and widely-separated, slightly prominent, transversely elongated, rhomboidal leaf-scars. " On the right-hand side, a thin carbonaceous layer probably represents the actual surface . . . On the partly decorticated surface there are discontinuous longitudinal ridges, and an irregular transverse wrinkling, but on the carbonized film no wrinkling is seen. There is no indication of any leaf-cushion, no ligular pit, and only a very faint suggestion in a few of the scars of a median vascular scar. The leaf-scars shown in the text-figure are rather more rounded and appear as slightly concave areas . . . In the small and widely-separated leaf-scars these fragments agree with *Bothrodendron*, *Pinakodendron*, and *Asolanus*. The form of the leaf-scar and the absence of a leaf-cushion are features more suggestive of *Bothrodendron*."

The features mentioned by Seward are those which are shown on the stems and larger branches of *Bothrodendron*, whereas clear leaf-cushions and leaf-scars of a more lepidodendroid form occur on the smaller branches. It is known that the gap between these two extreme forms is filled by a whole series of transitions. It is somewhat tempting to consider the three forms described by Seward as smaller branches and stems of the same species.

The last plant mentioned by Seward (1922, pl. 13, fig. 10) has not been named. This is represented by crowded branched filaments which are " probably portions of pinnules of a fern-like plant, such as some of the Lower Carboniferous species referred to *Rhodea* or *Sphenopteridium*."

Seward was at first inclined to regard his material as Upper Carboniferous in age. Dr. Kidston, however, regarded the palaeobotanical evidence as more favourable to a Lower Carboniferous horizon. After a re-examination of the specimens Seward modified his first opinion and agreed with Kidston. He remarks, however, that the plants are too imperfect to serve as trustworthy guides and that " further research is greatly to be desired, since the available data are inadequate as a basis for any positive statement."

Shortly after Seward's paper appeared, a fully illustrated account of the flora was published by Berry (1922). The determinations are discussed below :

### *Palmatopteris furcata* (Bgt.) Berry, 1922, pl. 1, figs. 1–3.

The plant he named *Palmatopteris furcata* is exceedingly common in the Paracas deposits. He unites with it *Sphenopteris affinis* (Steinmann, 1911 : 50) and *Sphenopteris hartlebeni* (Fuchs, 1900 : 50). These records certainly represent the same species, but it is not certain that the specific determination given by Berry is right. He does not give a detailed description and an opinion can be based only on his figures (pl. 1, figs. 1–3). The species has since been renamed *Sphenopteris paracasica* by Gothan (1928 : 293).

*Eremopteris peruianus* and *E. whitei* (Berry, 1922, pls. 2–4).

Berry describes two new species of *Eremopteris*. He points out the difficulties of demarcation between *Eremopteris* (especially as used by American authors) and *Rhacopteris*. He compares his *Eremopteris peruianus* (pls. 2, 3) with *Rhacopteris transitionis* (Ett.) as recorded by Stur (1875, pl. 8, figs. 5–7) but there are other species of " *Anisopteris* " with which Berry's material may be compared. According to his description and figures the size and form of the pinnules are very variable and it is quite likely that more than one species of *Rhacopteris* occurs in the material.

According to Berry his second species, *Eremopteris whitei*, is identical with *E. elegans* Lesquereux (1880, pl. 53, fig. 7). Berry considers this species to be entirely different from the European *Rhacopteris elegans* (Ett.) and from *R.* (*Sphenopteris*) *asplenites* Gutb. These European species have nothing in common with the Peruvian material.

Berry describes his material as follows : " The pinnae are linear oblong, their divisions or pinnules are oblique, oblong or rhomboidal in form, narrowed to the somewhat decurrent base, deeply pinnately cut by narrow sinuses into cuneate divisions which are rounded or subcrenate distad. The venation is flabellate and largely immersed in the thick substance of the lamina."

*Eremopteris whitei* Berry cannot be a *Rhacopteris* (sensu stricto) or *Anisopteris*. It might possibly be compared with some species of *Sphenopteridium* as figured by different authors (e.g., Walton, 1926) but Berry's figure alone is not sufficient to identify it with *Eremopteris* or *Rhacopteris*, and until further data are available it can be named *Sphenopteris whitei* (Berry).

It must have been a rather robust plant as evidenced by the stout longitudinally striated rachises. The nervation, as far as can be seen in Berry's figure, does not seem to agree with that of *Rhacopteris* or *Anisopteris* nor with *Eremopteris elegans* as figured by Lesquereux (1880, pl. 53, fig. 7) ; it can much better be compared with that of *Sphenopteridium*. Another plant with which it may be compared is that figured by me (1940, pl. 4, fig. 9) from the Lower Carboniferous of Egypt and erroneously referred to *Rhodea* cf. *hochstetteri* Stur. Better material which I received later shows that the Egyptian specimens cannot belong to Stur's species, and I now have little doubt as to their identity with Berry's species.

*Calamites suckowi* Bgt. (Berry, 1922, pls. 5–7).

The plants figured by Berry as *Calamites suckowi* Bgt. are very fragmentary and broken. Most of them do not show a nodal line. The best example is seen in pl. 6. Here a nodal line is present on which the sharply pointed ribs are clearly alternating, so that a reference to *Asterocalamites* is precluded. The stems undoubtedly belong to *Calamites*, but the sharply pointed ribs show that it cannot be *C. suckowi* ; it looks more like *C. undulatus* Sternb.

*Lepidodendron rimosum* Sternb. and *L. obovatum* Bgt. (Berry, 1922, pl. 8 ; pl. 1, fig. 5).

The two species of *Lepidodendron*, *L. rimosum* Sternb. (plate 8) and *L. obovatum* Bgt. (pl. 1, fig. 5) described and figured by Berry agree with Zeiller's opinion on this material (1917). It must be pointed out, however, that if Berry's figures agree with the originals there is a remarkable difference between pl. 1, fig. 5, and pl. 8, figs. 1, 2, on the one hand and pl. 8, fig. 3, on the other. Only in pl. 8, fig. 3, is a leaf-scar visible and it is likely that this drawing was not made from the figured specimens but included only to indicate Berry's conception of the species. His determinations will be discussed after reference to Gothan's paper.

*Lepidostrobus* sp. (Berry, 1922, pl. 1, fig. 4).

In his pl. 1, fig. 4, Berry figures a *Lepidostrobus*, described as " A characteristic *Lepidodendron* cone, too poor for identification or description." It is by no means certain that it is a *Lepidostrobus*. The cone is very similar to one figured by Johnson (1913, pl. 41, figs. 3, 4) as a cone or strobilus of *Bothrodendron kiltorkense*, but it does not show sufficient details to be certain of its identity.

Gothan (1928) described and figured some Carboniferous plants collected by Steinmann from Paracas and other localities to the north of this peninsula. Steinmann (1929) also dealt with this material. As many of the latter's figures are much clearer than those in Gothan's paper, the two can be considered together. A short review of the descriptions and discussions follows here :

*Rhodea* sp.

This is the form already recorded as *Rhodea filifera* by Steinmann (1911) and as Planta incertae sedis by Seward (1922). It is quite possibly a *Rhodea*, but specific determination is not possible.

*Sphenopteris paracasica* Gothan (1928, pl. 13, fig. 1) (including *Palmatopteris furcata* Berry, 1922, pl. 1, fig. 1 ; *Sphenopteris* sp. Seward, 1922, pl. 1, figs. 1, 2 ; Steinmann, 1929, text-fig. 30*a*, *b*).

Steinmann's figure is a copy of that in Gothan's paper, together with an enlargement of the pinnules. Seward, who notes the difference from *Palmatopteris furcata*, compares his material with *Rhodea* or *Sphenopteridium*, such as *S. norbergii* Nath., a species which its author compared with *Sphenopteris affinis*. Gothan compares it with *Adiantites bellidulus* Hr. (Nathorst, 1914, pl. 15, figs. 11–14). It is very probable that *Sphenopteris affinis* as recorded by Fuchs (1900) belongs to Gothan's species. Another species with which Gothan compares it is *Sphenopteris bodenbenderi* Kurtz (1921) from Carrizal, near Famatina, La Rioja. A comparison is also possible with some of the species described by Walton (1931, especially pl. 25, fig. 23) from the British Lower Carboniferous. The specimens known so far are too fragmentary for determination.

Nevertheless there is an important difference in the rachis as figured by Gothan and that figured by Seward. The former shows a rachis with a distinct middle line and no other ornamentation. Seward shows a rachis with a longitudinal striation. It is by no means certain that these two sets of specimens and those described by

Berry (no rachis and more penicillate pinnules) belong to the same species. There may be three different species, and so for the present it would be best to use Gothan's name *Sphenopteris paracasica* to indicate this type of plant.

*Rhacopteris circularis* Walton (Gothan, 1928, pl. 15, fig. 1).

Recorded from Vichaicoto, S. Huanuco, but not from Paracas, this is without doubt a *Rhacopteris*, though Gothan's specific determination may be questioned. Steinmann's fig. 29 includes a specimen which is comparable with that of Gothan's, together with some other figures of details of the leaves ; organs which he considers as aphlebia (D and E) ; and a fragment of a rachis (F), all found together with *R. circularis*. These figures, however, show details which are not completely identical with those in Gothan's figure.

The occurrence of *Rhacopteris* in these floras is very important. Berry (1922, pl. 2, figs. 1–3) described *Eremopteris peruianus* from Paracas, which almost certainly belongs to *Rhacopteris* and should be named *Rhacopteris peruianus* (Berry). It is possible, however, that it contains more than one species. The form of the pinnules is very variable, and as Gothan (1928 : 297) points out, it is probable that Berry's pl. 2, figs. 2, 3, especially fig. 3, belong to the plant which Gothan named *Rhacopteris circularis* Walton. If this is true the species has also been found in Paracas.

Berry's pl. 2, fig. 1 can be compared with *Rhacopteris petiolata* (Walton, 1926, pl. 16, fig. 10). For the present, however, Berry's name *Rhacopteris peruianus* must be retained, though new material may eventually show that it belongs to some previously described species.

*Calamites peruvianus* Gothan (1928, pl. 14, fig. 1).

Gothan illustrates some poorly preserved fragments of *Calamites* as a new species *Calamites peruvianus*, and considers Berry's *C. suckowi* as identical. As already pointed out (p. 195) these fragments belong to *Calamites* and not to *Mesocalamites* or *Asterocalamites*, since the ribs alternate regularly at the nodal lines. Their ends are not blunt as in *C. suckowi*, and Berry's figures show the sharp pointed ends of the ribs as in *C. undulatus*. Gothan supposes that these *Calamites* are only distantly related to the European species. However, the characters on which he bases this opinion (thin stems, with long and narrow internodes, without branch-scars or infranodal canal-traces) are characters which can be found in *C. undulatus* or which may be due to poor preservation and the fragmentary state of the specimens. There is no reason to create a new specific name for these fragments or to compare them with *Phyllotheca* or other genera of Equisetales. The specimen figured by Steinmann (1929, text-fig. 28) is even more fragmentary than those mentioned above. The only name which might be given is *Calamites* cf. *undulatus* Sternb., though the correct name should be *Calamites* sp. indet.

*Lepidodendron peruvianum* Gothan (1928, pl. 13, fig. 2).

This specimen is interesting as it does not show a leaf-scar. Gothan unites with this species *L. obovatum* and *L. rimosum* of Berry (1922, pl. 1, fig. 5 ; pl. 8, fig. 1

only). Berry's pl. 8, fig. 3 does not belong to this species, and most probably the drawing has nothing to do with the specimens figured on the same plate. In my opinion, however, Berry's pl. 8, fig. 2 should also be united with Gothan's species.

No leaf-scar is visible and the broad bands between the leaf-cushions point to *Lepidodendropsis*. The specimens may be compared with *Lepidodendropsis fenestrata* from the Lower Carboniferous of Egypt (Jongmans & Koopmans, 1940, pl. 2, figs. 4*a*–*c*). The only real difference is that those described by Berry and by Gothan are larger, and the leaf-cushions are broader and not so elongated. Gothan states that the surface of the bands which separate the cushions is smooth.

The figures published by Steinmann (1929, text-figs. 23A–D) are much better; they show clearly that the material belongs to *Lepidodendropsis* and the similarity to the Egyptian material is still more striking. The Peruvian species should therefore be named *Lepidodendropsis peruviana* (Gothan) Jongmans.

*Lepidodendron lissoni* Steinmann (Gothan, 1928, pl. 14, fig. 2).

Another species of *Lepidodendron* figured by Gothan (1928) and by Steinmann (1929, text-fig. 24) is *L. lissoni* Steinmann. Gothan compares it with *L. spetsbergense* Nath. So far as one can judge from the figure the specimen is badly preserved and it may be an older stem of *Bothrodendron*.

*Lepidodendron* sp. (Gothan, 1928, pl. 15, fig. 3, left).

It is not possible to give an opinion on this specimen. There may be some connexion with Seward's pl. 13, figs. 7, 8 (*Sigillaria* or *Lepidodendron*), but this will be very difficult to prove. Gothan also refers to a branch of *Lepidodendron* which he compares with Seward's pl. 13, figs. 4, 6. He does not figure the specimen.

*Asolanus* (?) *minimus* Gothan (1928, pl. 15, figs. 2, 2*a*, ? 3, right).

The material is insufficient for a true understanding of the plant which Gothan named *Asolanus* (?) *minimus*; it is not clear that it is an *Asolanus*. The ornamentation is more like that of *Bothrodendron* (or *Cyclostigma*) than of *Asolanus*.

? *Bothrodendron pacificum* Steinmann (Gothan, 1928, pl. 13, figs. 3, 3*a*).

Gothan compares his specimen with *Bothrodendron* sp. (Seward, 1922, pl. 13, fig. 9). It is very probable that Seward's figure represents a *Bothrodendron*– or *Cyclostigma*-like stem, but since all the leaf-scars in Gothan's figure are broken it is not possible to identify details of the scar. A ligule-scar could not be observed.

Fortunately Steinmann (1929, text-fig. 27) gives a much better picture of "*Bothrodendron*" *pacificum*. His figure is similar to Seward's fig. 4 and must belong to the same species. It follows that Steinmann's specific name *pacificum* can be used for Seward's (pl. 13, figs. 4, 7, 8), Gothan's (pl. 13, figs. 3, 3*a*) and Steinmann's figures. With the description of new material to be dealt with later in this paper, it will be shown that this species must be put into *Cyclostigma* and that Seward's fig. 9 is a bigger stem belonging to the same species. There is no trace of a ligule and therefore the material must belong to the eligulate group of the Lycopodiales.

*Trachyphyton neglegibile* Gothan (1928, pl. 14, figs. 3, 4).

It is difficult to give an opinion on Gothan's *Trachyphyton neglegibile*. He compares it with *Stigmariopsis*. No root-scars are visible, though these are often very indistinct in specimens of *Stigmariopsis*. Johnson (1914, pl. 15) figures some rhizomes of *Cyclostigma kiltorkense* which closely resemble Gothan's figure.

Gothan considers the flora to be of Lower Carboniferous age.

A further contribution to the Carboniferous flora of Paracas was published by Read (1938). It is based on material collected from the classic locality by H. Bassler in 1922. Bassler did not make a special exploration but picked only debris of rocks from a shallow shaft made by former collectors. Read records the following plants : *Sphenopteris "parasica"* Gothan ( = *S. paracasica*), *Adiantites whitei* (*Berry*), *Adiantites peruianus* (Berry), *Adiantites bassleri* Read, *Rhacopteris ovata* (McCoy) Walkom, *Rhacopteris* cf. *cuneata* Walkom, *Aphlebia australis* Read, *Lepidodendron peruvianum* Gothan and *Calamites peruvianus* Gothan.

The type of flora described by Read is much the same as that in earlier publications. Some of his determinations are discussed below.

*Adiantites whitei* (Berry) and *A. peruianus* (Berry) Read, 1938, text-fig. 3.

It is not entirely clear why Read includes *Eremopteris whitei* and *E. peruianus* in *Adiantites*. In my opinion it would be better to unite *E. peruianus* with *Rhacopteris*. I am not sure that Read's fig. 3 is the same plant as Berry's *E. peruianus* and I am inclined to compare it with *Triphyllopteris collombiana* Sch. As to *Eremopteris whitei* I prefer to leave this in *Sphenopteris* until better and more complete specimens have been found.

*Adiantites bassleri* Read (1938, text-fig. 7).

*Adiantites bassleri* Read is known only from a few fragments. They show the outline but no venation. This plant possibly belongs to the species which will be described as *Triphyllopteris collombiana* (Sch.) (p. 214).

*Rhacopteris ovata* (McCoy) Walkom (Read, 1938, text-fig. 1).

I entirely agree with Read's determination of his text-fig. 1 as *Rhacopteris ovata* (McCoy). As will be seen later, new material from the De Voogd collection clearly shows that this form is represented in the flora. The specimen figured by Gothan (1928, pl. 15, fig. 1) as *R. circularis* Walton does not show the same characters but they are seen in Steinmann's text-fig. 29, in Berry's pl. 2, fig. 3 (? 2), and in the specimens figured in this paper.

It is possible that Gothan's figure should be separated from the others and compared with *R. circularis* Walton, or it may be that the margins in Gothan's specimen are not well preserved.

It is curious that Read states that *Rhacopteris ovata* is very common in Paracas. So far as is known from the older literature there is only one figure from Paracas (Berry's *E. peruianus*, pl. 2, fig. 3; fig. 2 is very doubtful) which may be compared with *R. ovata*. Steinmann's specimens and Gothan's *R. circularis* Walton are from Vichaicoto, S. Huanuco.

*Rhacopteris* sp. cf. *R. cuneata* Walkom (Read, 1938, text-fig. 5).

A single fragment figured by Read as *Rhacopteris* sp. cf. *R. cuneata* may be correctly determined. Two fragments which resemble Read's figure will be described with the new material from Paracas belonging to the British Museum.

*Aphlebia australis* Read (1938, text-fig. 6).

This is a curious plant. It is a leafy, highly divided fragmentary organ ; the base is unknown. It is not possible to show a relationship with the other elements of the flora.

*Lepidodendron peruvianum* Gothan (Read, 1938, text-fig. 4).

Read's figure is not exactly like Gothan's pl. 13, fig. 2, and is more like Steinmann's figures. It is probable that this specimen belongs to *Lepidodendropsis*.

*Calamites peruvianus* Gothan.

Read mentions some specimens of *Calamites* which he unites with *C. peruvianus* Gothan. As already stated a specific name is unnecessary for these fragments.

In a paper on the fossil plants of the Neo-Paleozoic of Brazil, Read (1941 : 17) reviews the Mississippian floras of South America and gives a list of the Paracas flora according to his own observations. He records a similar flora collected from 10 km. N.E. of Garhuamayo, Peru. The collection is fragmentary and the following species are noted : *Rhacopteris ovata* (McCoy), *Adiantites bassleri* Read and *Lepidodendron peruvianum* Gothan.

He compares the flora with Lower Carboniferous floras from Argentina. Such a comparison could be made with success only after a revision of the floras of that country, since so many records from Argentina are in need of correction. It is clear, however, that the lower portion of the Carboniferous in Argentina has a similar *Rhacopteris*-flora, probably also with *Lepidodendropsis* to which almost certainly some of the *Lepidodendron* species listed from there may prove to belong.

Frenguelli (1943) was able to study some specimens of *Rhacopteris* from Carhuamayo, Peru, in the Museum of La Plata. (From this locality I received the specimens which are described in the last section of this paper). Frenguelli figures two specimens ; his pl. 3, fig. 1, is named *Rhacopteris circularis* Walton according to Gothan's determination and figure (1928, pl. 15, fig. 1), and his pl. 3, fig. 2 is named *R. ovata* and agrees with Steinmann's figures (1929, text-figs. 29A–C) and with Berry's pl. 2, fig. 3, and perhaps fig. 2 (1922). It is therefore probable that both species occur in the Lower Carboniferous of Peru.

In the same paper Frenguelli discusses specimens from Argentina. The specimen figured in his pl. 1 and the poorly preserved fragment in pl. 2, fig. 1, are from the Mine El Tupe, La Rioja, and those in pl. 4, figs. 1–3, are from Agua Salada, La Rioja ; these he names *Rhacopteris ovata* (McCoy). On pl. 4, fig. 4, he figures a specimen also from Agua Salada which he names *R. circularis* Walton. The difference between the two species is rather slight. It may be that the crenulate border of *R. ovata* is different from the more or less entire margin of *R. circularis* and that the form of the segments is somewhat different from those of *R. circularis* which are more circular. At all events it is interesting that the Argentine species of *Rhacopteris* agree with the Peruvian ones.

Frenguelli (1943, pl. 2, fig. 3 ; pl. 4, fig. 4) also figures specimens which he calls *Calamites peruvianus* Gothan, but they are equally as indeterminable as all or at least most of the other figures published under this name. It is useless to name or figure such bad specimens.

In an earlier paper Frenguelli (1941) also compares Peruvian plants with the flora of Argentina, describing an old collection of fossil plants from Agua de los Jejenes, San Juan. This flora is said to contain : *Rhacopteris semicircularis* Lutz, *R. ovata* (McCoy), *Eremopteris* cf. *sanjuanina* Kurtz, *E.* cf. *whitei* Berry, *Rhabdocarpus* ? sp., *Lepidodendron* cf. *veltheimianum* Sternb., and *Bothrodendron australe* Feistm.

*Rhacopteris semicircularis* was first described by Lutz (1933 : 144) from the Culm of Geigen near Hof. He compares it with *R. circularis* Walton, but considers it to be different. Frenguelli's figures (pl. 1, fig. 1 ; text-fig. 1) show the specimen which he compares with this species. He also compares it with *Cardiopteridium*, a comparison which is quite possible.

It is a pity that he did not figure his *Rhacopteris ovata* which he compares with Steinmann's *Rhacopteris circularis* Walton.

The specimen which Frenguelli (1941, text-fig. 2) compares with *Eremopteris sanjuanina* Kurtz resembles somewhat the specimens described later in this paper as *Triphyllopteris*. A revision of the Argentine plants will possibly show more comparisons with the Peruvian flora.

This is also the case with *Eremopteris* cf. *whitei* Berry (Frenguelli, 1941, text-fig. 3). His determination may be right, and if so, this is the first time that Berry's species has been recorded outside Peru.

The figure (pl. 1, fig. 2) which Frenguelli compares with *Lepidodendron veltheimianum* is indeterminable. There is no reason to accept a relation with *Lepidodendron*. Here we have another example of the well-known fact that so many of the specimens identified or compared with this, itself rather doubtful, species are absolutely valueless. The same is true for the specimen figured in his pl. 1, fig. 3, which he names *Bothrodendron australe* Feistm. and that in pl. 2 which he calls *Lepidodendron* sp.

## LIST OF THE CARBONIFEROUS FLORA OF PERU ACCORDING TO THE OLDER LITERATURE

As a preliminary result of this review of the older literature on the Carboniferous plants of Peru the following list of species is established :

*Calamites* cf. *undulatus* Sternb. (perhaps better as *Calamites* sp.). *C. suckowi* Bgt. (Berry, 1922) ; *C. peruvianus* Gothan (1928) ; ? *C. peruvianus* Read (1938) ; *C.* sp. Steinmann (1929, fig. 28).

*Cyclostigma pacifica* (Steinm.) Jongmans.

? *Bothrodendron pacificum* Steinmann (1929) ; *Lepidodendron* sp. Seward (1922) ; *Sigillaria* or *Lepidodendron* sp. Seward (1922) ; *Bothrodendron* sp. Seward (1922) ; "*Bothrodendron*" *pacificum* Gothan (1928).

"*Lepidodendron*" *lissoni* Steinmann (still doubtful).

*Lepidodendropsis peruviana* (Gothan) Jongmans.

*Lepidodendron peruvianum* Gothan (1928) ; Read (1938) ; *Lepidodendron obovatum* Bgt. (Berry, 1922) ; *Lepidodendron rimosum* Sternb. (Berry, 1922, excluding fig. 3).

*Asolanus* (?) *minimus* Gothan (still doubtful).

*Rhodea* sp. Steinmann.

*Rhodea filifera* Steinmann (1911) ; Planta incertae sedis Seward (1922).

*Sphenopteris paracasica* Gothan.

*Palmatopteris furcata* (Bgt.) Berry (1922) ; *Sphenopteris* sp. Seward (1922) ; *Sphenopteris* "*parasica*" Read (1938).

*Sphenopteris whitei* (Berry) Jongmans.

*Eremopteris whitei* Berry (1922) ; *Sphenopteris hartlebeni* Dkr. (Fuchs, 1900) ; ? *Sphenopteris affinis* (Steinmann, 1911) ; *Adiantites whitei* (Berry) Read (1938).

*Rhacopteris* cf. *circularis* Walton.

*Rhacopteris circularis* Walt. (Gothan, 1928) ; Frenguelli (1943).

*Rhacopteris ovata* (McCoy) Walkom.

*Rhacopteris circularis* Walt. Steinmann (1929) at least very probable for the crenulate margin ; *Eremopteris peruianus* Berry (1922, pl. 2, fig. 3 and probably fig. 2) ; *Rhacopteris ovata* (McCoy) Frenguelli (1943).

*Rhacopteris* cf. *R. cuneata* Walkom.

*Rhacopteris* cf. *cuneata* Walk. (Read, 1938).

*Rhacopteris peruiana* (Berry) Jongmans.

*Eremopteris peruiana* Berry (1922, pl. 2, fig. 1 only) [not *Adiantites peruianus* (Berry) Read (1938)].

cf. *Triphyllopteris collombiana* (Schimper).
Probably *Adiantites peruianus* (Read, 1938, text-fig. 3).
Possibly *Adiantites bassleri* Read (1938, text-fig. 7).

*Aphlebia australia* Read (1938).

Berry's *Lepidostrobus* (1922, pl. 1, fig. 4) resembles a cone of *Cyclostigma kiltorkense* figured by Johnson (1913, pl. 41, figs. 3, 4), and Gothan's *Trachyphyton neglegibile* is very much like Johnson's figures of the rhizome of the same plant.

The age of the flora is considered to be Lower Carboniferous by Steinmann, Seward (and Kidston), Gothan and Frenguelli. The only plant which could indicate a Namurian or Westphalian age is *Calamites* cf. *undulatus*. However, the specimens of *Calamites* recorded from Paracas are almost always indeterminable. Only in one case does it seem to resemble in some respects *Calamites undulatus*.

Berry (1931 : 295) considers the flora as of Westphalian age, and if the floral list given by him could be accepted, he certainly would be right. However, there are many mistakes and wrong identifications in his list, and the revised list of the specimens described by him definitely indicates a Lower Carboniferous flora.

The arguments of Gothan, Seward (Kidston), Steinmann, Read, and Frenguelli are so weighty that there can be little doubt as to the lower Carboniferous age of the flora. The description of the new collections will supply further evidence in favour of their arguments.

## A NEW COLLECTION FROM PARACAS

Many years ago the Trustees of the British Museum, by the kind intermediance of Mr. W. N. Edwards, placed a new collection from this Peninsula at my disposal for study. The plants were collected by the late Professor J. W. Gregory, whose untimely death by drowning in a canoe accident in the rapids of the river Urubamba at the age of 68 occurred, during an expedition to Peru, on 2nd June, 1932.

### **Sphenopteris whitei** (Berry) Jongmans

(Pl. 17, figs. 1–4)

? 1900. *Sphenopteris hartlebeni* Dunk.: Fuchs, p. 50.
? 1911. *Sphenopteris affinis* L. & H.: Steinmann, p. 50.
1922. *Eremopteris whitei* Berry, p. 20, pl. 4.
1938. *Adiantites whitei* (Berry) Read, p. 401.
? 1940. cf. *Rhodea hochstetteri* Stur: Jongmans & Koopmans, p. 228, pl. 4, fig. 9.
? 1941. *Eremopteris* cf. *whitei* Berry: Frenguelli, p. 470, text-fig. 3.

Occurrence. Paracas, Peru; Agua de los Jejenes, Argentina; Rhas Gharib, Egypt.

The collection includes a rather large number of specimens containing fragments of a plant which may be determined as *Sphenopteris whitei* (Berry). Some of them are figured here to prove their identity with those figured by Berry (1922) as *Ere-*

*mopteris*. There is no doubt about the agreement. The specimens do not show any remarkable or new details. The form of the pinnules agrees with Berry's figure. The venation, however, is not very clear. Amongst the numerous figures with which these fragments may be compared is *Rhodea hochstetteri* Stur (Jongmans & Koopmans, 1940, pl. 4, fig. 9) from the Lower Carboniferous of Egypt which is almost certainly identical with Berry's species. Better examples of the Egyptian material (collected more recently) will be described in a separate paper.

Other specimens belonging to this species are: V.25913, V.25934, V.25935, V.25937–39, V.25941–47.

### ***Cyclostigma pacifica*** (Steinmann) Jongmans

(Pl. 17, figs. 5–7; Pl. 18, figs. 8–10; Pl. 19, figs. 11–14; Pl. 20, figs. 14$b_{2,3}$)

1922. *Lepidodendron* sp. Seward, p. 280, pl. 13, figs. 4–6.
1922. *Sigillaria* or *Lepidodendron* sp. Seward, p. 280, pl. 13, figs. 7, 8.
1922. *Bothrodendron* (?) sp. Seward, p. 281, pl. 13, fig. 9; text-fig.
1928. *Bothrodendron pacificum* Steinmann: Gothan, p. 296, pl. 13, figs. 3, 3*a*.
cf. 1928. *Lepidodendron* sp. Gothan, p. 295, pl. 15, fig. 3.
1929. *Bothrodendron pacificum* Steinmann, p. 31, text-fig. 27.

Small branches with very approximate prominent leaf-cushions with a somewhat elliptical leaf-scar without cicatricules. Ligule not visible. Distance between the cushions very variable, even on the same specimen. Cushions separated by vertical, sharp, undulated lines, so that there is always an open communication between the succeeding cushion-fields in the vertical row. Scars rounded in the upper half, lower half consisting of two lateral sides meeting in a sharp point. In older stems the distance between the scars is much greater, and the contours of the cushions disappear as the distance increases. Surface of older stems smooth or ornamented with undulating lines. Leaves long, narrow, and sharply pointed, with a distinct midrib (Seward, 1922, pl. 13, figs. 4, 6).

DESCRIPTION. The collection contains numerous branches and small and large stems. Several of the smaller stems belong to the same type and can be compared with those figured by Seward (1922, pl. 13, figs. 4, 7, 8) and by Steinmann (1929, text-fig. 27).

Unfortunately most of the specimens do not show the true leaf-scars as the prominent cushions are always broken at the tips. There are, however, strong indications that these stems bore somewhat elliptical scars. The lines separating the cushions are undulate but they are not always well marked, and in some cases the form of the cushions is irregular and crushed (see Seward, 1922, pl. 13, figs. 7, 8). This can be seen in Pl. 17, figs. 5, 6. Pl. 17, fig. 5*a*, is interesting as it shows the form of the leaf-scar very clearly, and this is also visible on specimen V.25929. Pl. 17, figs. 6, 7 and Pl. 18, figs. 8, 8*a*, show that the distance between the leaf-cushions is very variable, and this is even more so in Steinmann's text-fig. 27 which also shows that there are areas on the branches where the distance is much smaller than usual. Specimens V.25922, V.25924, V.25926 and V.25927 all belong to this type but are not so well preserved.

At first sight it seems somewhat peculiar that the leaf-cushions figured by Seward (1922, pl. 13, figs. 7, 8) belong to the same plant as his fig. 4. However, Pl. 17, fig. 5, and Pl. 18, fig.8, show that both types are present on the same specimen. It is possible that there are irregularities in the form of the cushions such as those seen in *Sigillaria* in regions where the large scars bearing the fructifications are found, or it may be that there is some difference between succeeding regions of stems and branches as is known from other species of *Sigillaria* in connexion with differences in the mode of growth (cf. Potonié, 1894). A similar difference is also present in *Bothrodendron leslii* Seward, in *Sigillaria mutans* Weiss, and in Steinmann's text-fig. 27.

One of the best specimens, with part of its counterpart, is shown in Pl. 18, figs. 9, 10. It shows stems on both sides. The branch in fig. 9 can be compared with Seward's fig. 4. In the photograph the cushions are not always distinctly visible, but the undulated lines between the vertical rows are well seen in several places.

The true scars are well preserved on the counterpart (Pl. 18, figs. 10, 10*a*). The separation of the rows of cushions is indicated by a very delicate undulated line, so that the leaf-cushions are situated in the centre of the broadest part which is narrowed up- and downward. There is always an open communication between the succeeding cushion-fields in the vertical rows. The real scar lies in a deep hollow of the impression (in reality an elevation). Over and under the scars and cushions there is a distinct smooth field. There is no special ornamentation on the rest of the cushions. These characters are very well seen in Pl. 17, fig. 5. No cicatricules or ligule are visible.

As already stated the space between the cushions and scars is variable. In Pl. 17, fig. 7, the space is considerable. At the same time the lines separating the vertical rows are less distinct and disappear, the characters of the cushions also decrease, and the more or less isolated scars are all that remains of the former structure. The form of the scar itself does not change very much ; it is somewhat more regularly elliptical. This is well seen in Pl. 19, figs. 11, 12. and in the counterpart specimen (V.25933). A very good example of this type is shown in Pl. 19, fig. 13 ; here the form of the leaf-scars is clearly visible. They have about the same form as those seen in Pl. 17, fig. 5 and Pl. 18, fig. 10. Another good example is given in Pl. 19, fig. 14, which can be compared with Seward's pl. 13, fig. 9.

That the isolated scars originally had the same form as that shown in Pl. 18, fig. 8 can be seen on the right of Pl. 19, fig. 11, where the elongated cushions and the undulating lines which separate them are visible.

The surface between the scars is smooth (or almost smooth) in the specimen figured by Seward (1922, pl. 13, fig. 9) and in that figured in Pl. 19, fig. 11. However, the specimens shown in Pl. 19, figs. 12, 14 are remarkable for a distinct ornamentation on the surface between the scars. This ornamentation consists of delicate longitudinal lines, a number of which converge towards the scars, and recalls that of *Bothrodendron*. As the ornamentation is not always visible it may be that its presence or absence is due to the layer which is preserved on the fossil. The ornamentation is somewhat similar to that figured by Gothan (1928, pl. 15, figs. 2*a*,

3) in his *Asolanus* (?) *minimus*. In the British Museum specimens the arrangement is visible in oblique lines and less distinctly in horizontal lines.

It is clear that, as in the case of the Westphalian species of *Bothrodendron*, *Cyclostigma kiltorkense*, and some species of *Lepidodendropsis*, the leaf-cushions on the young branches are very distinct, approximated, and more or less separated by dividing lines, so that they have a lepidodendroid aspect. On the lower parts of the branches and on the stems this lepidodendroid character decreases and disappears. The result is that the leaf-scars are placed on a rather smooth or delicately ornamented surface (Seward, 1922, pl. 13, fig. 9). This stage is seen in the specimen (with its counterpart) shown in Pl. 19, figs. 12, 14. An excellent specimen of this type is figured in Pl. 19, fig. 14*b*. One part of the specimen shows a not very distinct ornamentation between the scars, another part is almost smooth but shows the scars very well. The scars have the same form as those in Pl. 17, figs. 6, 7, but are much better preserved. The specimen represented in Pl. 19, fig. 11, is, in some respects, transitional between the extremes.

Rarely the leaves are still attached to the branches. The best examples are shown in Seward's pl. 13, figs. 4, 6; the leaves are long, narrow and sharply pointed, with a distinct midrib. The specimens show fragments of leaves rarely or not at all.

This species must belong to *Cyclostigma* and not to *Bothrodendron*, for the form of the leaf-cushions and their arrangement on the younger branches are entirely different from the latter and no ligule or cicatricules can be found. Steinmann's specific name *pacificum* must be retained, and therefore the correct name for these plants is *Cyclostigma pacifica* (Steinmann) Jongmans.

Specimens similar to those figured in Pl. 19, figs. 12, 14, with ornamentation on the surface between the leaf-scars, may be distinguished as var. *decorata*, although as stated above the presence or absence of this ornamentation may be due to preservation.

Regarding the determination of this plant as *Cyclostigma*, the "*Lepidostrobus*" figured by Berry (1922, pl. 1, fig. 4) and the peculiar specimen described and figured as *Trachyphyton neglegibile* by Gothan (1928, pl. 14, figs. 3, 4) may be important. The *Lepidostrobus* can be compared with the figures of cones of *Cyclostigma kiltorkense* in Johnson's paper (1913, pl. 14, figs. 3, 4) and Gothan's figures with those of the rhizome of this plant figured by the same author (Johnson, 1914, pls. 14, 15). It may yet be proved that these or similar organs belong to *Cyclostigma pacifica* or an allied species.

## Genus ***LEPIDODENDROPSIS*** Lutz

### ***Lepidodendropsis peruviana*** (Gothan) Jongmans

### (Pl. 20, fig. 15)

1922. *Lepidodendron rimosum* Sternb.: Berry, p. 24, pl. 8, figs. 1, 2 only.
1922. *Lepidodendron obovatum* Brongn.: Berry, p. 26, pl. 1, fig. 5.
1928. *Lepidodendron peruvianum* Gothan, p. 294, pl. 13, fig. 2.
1929. *Lepidodendron peruvianum* Gothan: Steinmann, p. 30, text-fig. 23A–D.
1938. ? *Lepidodendron peruvianum* Gothan: Read, pp. 398, 402, text-fig. 4.

Description. As stated above the specimens identified as *Lepidodendron peruvianum* by Gothan (1928) and by Steinmann (1929) belong to *Lepidodendropsis*. Three examples of this species are in the British Museum collection (V.25911, V.25912 and V.25931). The best specimen is that seen in Pl. 20, fig. 15. Form and arrangement of the cushions agree with those figured by Gothan (1928, pl. 13, fig. 2) and by Steinmann (1929, text-fig. 23). There is, however, a slight difference. According to their figures and descriptions the surface of the bands separating the leaf-cushions is smooth. This is not the case in the new specimens, where some rather coarse longitudinal or almost longitudinal lines are present. This difference may be essential or may be due to the state of preservation. At all events, the comparison made between this species and the Egyptian *Lepidodendropsis fenestrata* Jongm. & Koopm. increases in probability.

### ***Lepidodendropsis ("Lepidodendron") lissoni*** (Steinmann) Jongmans

(Pl. 20, fig. 16)

1928. *Lepidodendron lissoni* Steinmann: Gothan, p. 295, pl. 14, fig. 2.
1929. *Lepidodendron lissoni* Steinmann, p. 31, text-fig. 24.

Description. The British Museum collection contains a specimen (V.25932) which may belong to the same species as that figured by Gothan (1928) and by Steinmann (1929). Gothan compares the species with *Lepidodendron spetsbergense* Nath. The specimen is distinguished by the peculiar field under the scars. It may be that such fields are the remains of lepidodendroid cushions, and it is probable that this plant belongs to *Lepidodendropsis*, in which case it might be compared with *Lepidodendropsis cyclostigmatoides* Jongmans, Gothan & Darrah (1937, pl. 50, fig. 28). Since no true *Lepidodendron* has been found in the flora of Paracas it is safer to use the name *Lepidodendropsis* ? *lissoni* (Steinmann) Jongmans. Better specimens are necessary before a final decision is possible.

### ? ***Lepidodendropsis*** sp.

(Pl. 20, fig. 17)

This remarkable specimen (V.25915) shows two large branches or stems, at least 7–8 cm. broad. They are covered with cushions very similar to those of *Lepidodendropsis*. No real leaf-scar is visible. One of the stems shows fragments of the leaves attached to it, and it is clear that in this species the leaves were very persistent. Although it is almost certain that the specimen belongs to an undescribed species, the details are too poorly preserved for specific determination.

### ***Rhacopteris*** cf. ***cuneata*** (Walkom)

(Pl. 20, fig. 18)

1938. *Rhacopteris* cf. *cuneata* (Walkom): Read, p. 401, text-fig. 5.

Two small specimens (counterparts, V.25948) can be compared with *Rhacopteris* sp. cf. *R. cuneata* (Walkom) figured by Read (1938, text-fig. 5). The specimens are illustrated in Pl. 20, figs. 18, 18*a*, 18$a_1$. The occurrence of a very small fragment of *Rhacopteris ovata*, which can be seen at the top left corner of Pl. 20, fig. 18*a*, is interesting. The only previously recorded specimen of *Rhacopteris ovata* from Paracas is that figured by Berry (1922, pl. 2, figs. 2, 3) as *Eremopteris peruviana*. Better examples of this species are known from Vichaicoto, S. of Huanuco, Peru (Steinmann, 1929, text-fig. 29) and from Peru and Argentina (Frenguelli, 1943, pls. 1–4).

It is curious that the present collection does not contain specimens of *Rhacopteris circularis* nor, except for the fragment referred to, of *Rhacopteris ovata* which must, however, belong to the more common elements of the Peruvian flora.

### ***Asolanus*** **(?)** ***minimus*** Gothan

1928. *Asolanus* (?) *minimus* Gothan, p. 295, pl. 15, figs. 2, 2*a*, ? 3 right.

The collection contains two small fragments (V.25909 and V.25910) which may be compared with Gothan's species. Unfortunately the preservation is too bad for the specimens to be figured.

From the flora represented in the British Museum collection it follows that although the number of species is relatively small, it provides more and better evidence regarding several of these species.

The full list of the flora so far known from the Paracas Peninsula contains the following species :

*Calamites* sp. (cf. *undulatus* Sternb.).
*Cyclostigma pacifica* (Steinm.).
*Lepidodendropsis peruviana* (Gothan).
*Lepidodendropsis* sp.
*Lepidodendropsis* ? *lissoni* (Steinm.).
*Asolanus* ? *minimus* Gothan.
*Rhodea* sp.
*Sphenopteris paracasica* Gothan.
*Sphenopteris whitei* (Berry).
*Rhacopteris ovata* (McCoy).
*Rhacopteris* ? *circularis* Walton.
cf. *Rhacopteris cuneata* (Walkom).
cf. *Triphyllopteris collombiana* (Sch.)
*Adiantites bassleri* Read (*Triphyllopteris*).
*Aphlebia australis* Read.
" *Lepidostrobus* " sp. Berry (? *Cyclostigma*).
*Trachyphyton neglegibile* Gothan (? *Stigmaria*, ? *Cyclostigma*).

The British Museum collection provides further proof that the flora of Paracas must be of Lower Carboniferous age. The aspect of the flora is similar to that of the Lower Carboniferous of Egypt and of the Pocono in U.S.A., although there are minor differences; thus *Rhacopteris* of the Peruvian type is not yet known from Egypt or the Pocono formation.

## FLORA OF CARHUAMAYO

Dr. De Voogd, one of my former assistants, sent me a good collection of plants from the neighbourhood of Cerro de Pasco at Carhuamayo. With the exception of the specimens of *Rhacopteris* figured by Frenguelli (1943) no descriptions or figures of plants from this locality have so far been published. Read (1941 : 17) mentions a florule from this locality containing *Rhacopteris ovata* (McCoy), *Adiantites bassleri* Read (possibly identical with his figure (1938 : 402, text-fig. 7) from Paracas, belonging to *Triphyllopteris*), and *Lepidodendron peruvianum* Gothan (erroneously ascribed by the author to Berry & Read) which probably belongs to *Lepidodendropsis peruviana* (Gothan).

The new collection is important for the remarkable forms of *Lepidodendropsis* and the very good specimens of *Rhacopteris* and *Triphyllopteris*.

### *Lepidodendropsis de voogdi* n. sp.

(Pl. 21 ; Pl. 22, figs. 24–27 ; Pl. 25, fig. 32 ?)

DIAGNOSIS. Stems with leaves, sometimes with sporangia. Stems with scars of *Lepidodendropsis* type, covered by the basal parts of the leaves. Scars numerous. Distance between scars small. Leaves spreading, 3 cm. or more long, up to 5 mm. broad, acuminate, with a distinct middle nerve. Sporangia, containing megaspores, visible in the axils of the leaves.

DESCRIPTION. Pl. 21, fig. 19 shows the axis and leaves (or sporophylls) of a specimen which make a somewhat lepidodendraceous impression. The axis is very broad. The scars, badly preserved, are placed in obliquely ascending lines. The horizontal and vertical arrangements are both distinct, but the oblique arrangement is most striking. Numerous leaves (or sporophylls) are connected with the axis. They are 3 cm. or more long and up to 5 mm. broad, acuminate, with a distinct middle nerve. The lower (sporangium-bearing) part is rather short, about 5 mm. long, and increases in breadth towards the implantation of the axis. This basal part is not very clearly separated from the rest. The leaves are spreading and very crowded. They resemble a *Lepidophyllum* of the *lanceolatum* type.

A second specimen (Pl. 21, fig. 20) is much longer. It shows the sporophylls, but the form of these is not so well seen. The most interesting part of this specimen is where the large, *Lepidostrobus*-like sporangia are visible on the outer left and right sides. They are 3–4 mm. broad and about 2 mm. high. Their size agrees with the basal part of the sporophylls in the first specimen. The specimen shows that the sporangium-bearing part of the sporophyll is almost horizontal and that the free part is abruptly erect.

The form of the scars on the broad axis is not visible, probably due to fragments of the sporophylls which more or less cover them. As far as can be seen, they appear to be almost elliptical.

A specific determination of the strobilus, or perhaps sporophyll bearing branches is of considerable importance. In this respect a specimen with similar leaves, but with no sporangia present (Pl. 21, figs. 21, 21*a*) is of value. It shows two leaf-bearing branches, one of which, the branch on the left (Pl. 21, fig. 21*a*), shows scars which agree completely with the small scars of *Lepidodendropsis*.

Another branch shows a bifurcation (Pl. 21, figs. 22, 22*a*). The scars are oval elliptical and are about the same size as those shown in Pl. 21, figs. 21, 21*a*. The leaves are broken. In the axils of the leaves are the remains of sporangia which contain megaspores.

This specimen is clearly a fructification which does not form a true strobilus and which agrees in this respect with *Lepidodendropsis vandergrachtii*. The latter species differs, however, as in *Pinakodendron*, in the absence of lepidodendroid sporangia which are present in the Peruvian material. On the back of this specimen two fragments of branches are visible both with long leaves attached (Pl. 21, fig. 23). One, on the left, without, the other, on the right, probably with sporangia and spores.

Another specimen (Pl. 22, fig. 24) shows two fragments of branches, both with well-preserved leaves and probably sporangia and spores. The leaves show the general form of those in Pl. 21, fig. 19, but they appear to be somewhat narrower. Pl. 22, fig. 25, shows a narrow branch with very long leaves of the same type. There is no trace of sporangia or spores.

A somewhat curious specimen (Pl. 22, fig. 27) shows leaves only without a trace of the branches or stems. The specimen figured in Pl. 22, fig. 26 shows isolated leaves which are unusually narrow.

This plant undoubtedly belongs to *Lepidodendropsis*. It is here named *Lepidodendropsis de voogdi* after Dr. De Voogd who collected the material for me.

### ***Lepidodendropsis*** cf. ***de voogdi*** Jongmans

(Pl. 25, fig. 32)

This specimen has no leaf-scar and the " cushion " is of the *Lepidodendropsis* type. It is possible that it belongs to one of the other species, but it may be different. It can be compared with *Lepidodendropsis de voogdi* (Pl. 21, fig. 21) which shows the same type of leaf-bases.

### ***Lepidodendropsis steinmanni*** n. sp.

(Pl. 22, figs. 28*a*, *d*; Pl. 23, figs. 28*b*, *c* ; ? Pl. 24, fig. 31)

DIAGNOSIS. Large stem, more than 3·5 cm. broad, covered by small " cushions." Horizontal distance between two cushions about 0·8 cm., oblique distance 4–5 mm. Vertical distance variable. Cushions occasionally more crowded, very small and not very distinct, indicated by smooth, almost triangular spaces (probably representing the basal parts of the leaves attached at the top of the " cushions "). Leaves attached at the " cushions " with their full base ; on leaving the stem they are first directed downwards and then obliquely erect.

DESCRIPTION. A second species of *Lepidodendropsis* is represented by a large stem with counterpart. Between these two parts a fragment of the pith cast is present (Pl. 22, fig. 28*d*). The stem is rather broad, somewhat more than 3·5 cm. wide and covered by small " cushions " (Pl. 22, fig. 28*a*) arranged in ascending lines. The arrangement in horizontal lines is not very distinct. The horizontal distance between two cushions is about 0·8 cm., the oblique distance 4–5 mm. The distance between the scars is not always the same. In at least two places they are more crowded, as in *Lepidodendropsis vandergrachtii* from the Pocono. The best "cushions " can be seen at the top of the figure. They are very small and agree generally with those of *Lepidodendropsis* (Pl. 23, fig. 28*c*) ; a cushion is indicated by a smooth, almost triangular space. A leaf-trace is not visible, and the upper part of the " cushion " bends into the rock over the upper limit of the " cushion." The space between the cushions is finely granulated (chagrinate) and almost smooth (Pl. 23, fig. 28*c*).

The pith-cast is covered by a thin coal-layer which is somewhat more distinctly chagrinate than the impressions. This delicate ornamentation is also visible on the actual surface of the pith-cast (Pl. 22, fig. 28*d*).

The stem bears narrow leaves which are specially well seen on the upper part. The leaves are directed downwards for about 4 mm. as they leave the stem, but from there they are abruptly erect.

This species agrees rather well with *Cyclostigma ungeri* Jongmans, Gothan & Darrah (1937, pl 57, figs. 45, 45*a*). Here too the horizontal lines in the arrangement of the cushions are much less developed than the very distinct oblique lines, and the surface bears a very delicate ornamentation. This ornamentation is different, however, and the cushions are larger, not so punctiform, and the horizontal and vertical distances between the cushions are much greater.

The leaf-cushions of the Peruvian specimens do not agree with those of *Cyclostigma* and more closely resemble those of *Lepidodendropsis*. A true leaf-scar is not visible.

In the description of *Cyclostigma ungeri* it was pointed out that it was only provisionally compared with that genus. It probably belongs to *Lepidodendropsis*.

The new name *Lepidodendropsis steinmanni* is provisionally proposed for the Peruvian species.

### ***Lepidodendropsis*** cf. ***steinmanni*** Jongmans

(Pl. 24, fig. 31)

In this specimen the leaf-cushions are similar in form to those of *Lepidodendropsis steinmanni* but they are much larger. It may be an older stem of this species and is named *Lepidodendropsis* cf. *steinmanni* accordingly.

### ***Cyclostigma pacifica*** (Steinmann)

(Pl. 24, fig. 30)

A small specimen belonging to this species may be compared with those figured by Seward (1922, pl. 13, figs. 4, 6). It shows the shape of the cushions and also fragments of the leaves. It is remarkable that this is the only specimen in the new collection which undoubtedly belongs to this species.

### ***Cyclostigma* cf. *pacifica*** (Steinmann) var.

(Pl. 23, fig. 29*a*; Pl. 24, fig. 29*b*, *c*)

A plant which probably belongs to *Cyclostigma* is represented by a small fragment found in the same block as the specimen figured in Pl. 22, fig. 28. It consists of the impression of the upper and lower sides of the stem and a part of the pith-cast (Pl. 23, fig. 29*a*; Pl. 24, fig. 29*b*, are from the upper and lower surfaces, Pl. 24, fig. 29*c*, from the pith-cast).

The leaf-cushions have the same form as those found in *Cyclostigma pacifica*. The only difference is that they are much more flattened, and are not so prominent as in most of the specimens of that species. The surface of the cushions is not smooth. There are also fragments of leaves which are shown in Pl. 24, fig. 29*b*, *c*.

A detailed description seems unnecessary since the figures show the details rather well. The lines separating the cushions are delicate but sharp and are well seen in several places (Pl. 23, fig. 29*a*, left side; Pl. 24, fig. 29*b*). The leaf-scars are placed in the centre of the cushions. The surface is finely chagrinate.

It is very probable that this plant is specifically identical with *Cyclostigma pacifica* and it is therefore described as *C.* cf. *pacifica* var. until more complete specimens are available for study.

### ***Rhacopteris ovata*** (McCoy) Walkom

(Pl. 25, figs. 33–37; Pl. 26, fig. 45)

1922. *Eremopteris peruianus* Berry, p. 19, pl. 2, fig. 3, ? fig. 2.
1929. ?*Rhacopteris circularis* Walton: Steinmann, p. 33, text-fig. 29 A–C.
1938. *Rhacopteris ovata* (McCoy): Read, p. 401, text-fig. 1.
1943. *Rhacopteris ovata* (McCoy): Frenguelli, pp. 14, 22, pl. 1; pl. 2, fig. 1; pl. 4, figs. 1–3 (Argentina); Pl. 3, fig. 2 (Carhuamayo).

OCCURRENCE. Paracas; Vichaicoto, S. Huanuco and Carhuamayo, Peru. El Tupe, La Rioja, Argentina.

As in Vichaicoto, S. of Huanuco, specimens of *Rhacopteris* of different sizes are very common at this locality. Some of them are excellently preserved.

In many cases it is not easy to distinguish the two species *Rhacopteris circularis* and *Rhacopteris ovata*. The chief differences are the margins and the form of the pinnules. In typical specimens the margins of *Rhacopteris ovata* are crenulate and the form of the pinnules is distinctly asymmetric and not circular. However, in Walton's description of *Rhacopteris circularis* (1926: 208) he states "Margin of pinnules entire, more rarely crenulate or lobed. Pinnules circular to semi-flabelliform. There is a tendency to asymmetry in the higher pinnules on the frond." It is possible that in most cases the smaller specimens show the characters of *R. circularis* and the larger ones those of *R. ovata*. Frenguelli (1943) figures specimens which he ascribes to both species. His figures of *R. ovata* (pl. 1; pl. 3, fig. 2; pl. 4, figs. 1–3, especially fig. 2) show the characters of *R. ovata* very well, with crenulate, asymmetric large pinnules.

Frenguelli's pl. 3, fig. 1, shows rounded pinnules and no crenulation, whereas the specimen in pl. 4, fig. 4, shows pinnules even more rounded and slightly asymmetric, also without crenulation. In some respects this latter specimen is transitional between the two extreme types.

Berry's figures (1922, pl. 2, fig. 3 and possibly fig. 2) show the characters of *R. ovata*. Steinmann's figures (1929, text-figs. 29*a–c*) can also be identified with this species, but Gothan's figure (1928, pl. 15, fig. 1) is somewhat doubtful; most of the pinnules are incomplete and it is possible that they may have been more rounded. As far as can be seen there is no crenulation. The specimen figured by Read (1938, text-fig. 1) also shows the characters of *R. ovata*.

Amongst the figures of *R. ovata* in the older literature is an interesting specimen figured by Dun (1905, pl. 23). This specimen is very long, the lower part of the pinna shows the large, crenulate and more or less asymmetric pinnules typical of *R. ovata*, whereas the upper part of the pinna shows much smaller symmetric pinnules with distinctly circular upper margins. Similar small pinnules are also represented in Dun's pl. 22, fig. 3.

Several of the specimens figured by Feistmantel (1890) do not show the crenulated margin and some of them are more or less circular (e.g., specimens in pl. 4), whereas others agree more closely with *R. ovata* (pl. 5, fig. 2; pl. 8; pl. 9, especially fig. 2). Some crenulation is indicated in his pl. 7, fig. 1.

Walton's figures of *R. circularis* generally show a uniform character in the shape of the pinnules, which is never or very rarely found in specimens of *R. ovata*. Therefore I am inclined to consider most of the Peruvian specimens as belonging to *R. ovata*.

In most of the specimens the margins of the pinnules are not preserved or have been broken off or hidden in the rock. This is the case with much of the present material, although, on most of these specimens, the crenulation is visible somewhere. The shape of the pinnules differs considerably. An extreme type is the large specimen shown in Pl. 25, fig. 33. A number of specimens (Pl. 25, figs. 34–37) show pinnules of different sizes, and some of them show the venation quite well.

### ***Rhacopteris* cf. *circularis* Walton**

(Pl. 25, fig. 38; Pl. 26, fig. 39)

1928. *Rhacopteris circularis* Walton: Gothan, p. 293, pl. 15, fig. 1.
1943. *Rhacopteris circularis* Walton: Frenguelli, pp. 22, 41, pl. 3, fig. 1; pl. 4, fig. 4.

OCCURRENCE. Carhuamayo and Vichaicoto, Peru. Agua Salada, La Rioja, Argentina.

A fine specimen of *Rhacopteris* is represented in Pl. 25, fig. 38. Here most of the pinnules have more or less rounded margins and their dimensions are very variable. It is interesting to note that the pinnules show a distinct footstalk, as in Walton's figures of *Rhacopteris circularis*. If *R. circularis* is present in the Peruvian flora, then this specimen may be considered to belong to it. Feistmantel's figured specimens with margins and pinnules typical of *Rhacopteris ovata* do not possess such a distinct leaf stalk. It is possible that the specimen figured in Pl. 26, fig. 39, which has rather distinct leaf stalks also belongs to *Rhacopteris circularis* Walton.

## Genus ***TRIPHYLLOPTERIS*** Schimper

This genus is well represented in the collection from Carhuamayo. Three forms can be distinguished and they may belong to different species.

### ***Triphyllopteris collombiana*** (Schimper)

(Pl. 26, figs. 40–42)

? 1938. *Adiantites peruianus* (Berry) Read, p. 401, text-fig. 3.
? 1938. *Adiantites bassleri* Read, p. 399, text-fig. 7.
1941. cf. *Eremopteris* cf. *sanjuanina* Kurtz : Frenguelli, p. 468, text-fig. 2.

OCCURRENCE. Paracas and Carhuamayo, Peru ; Agua de los Jejenes, Argentina.

A rather large form is represented by several specimens of which Pl. 26, figs. 40–42, are typical examples. These specimens resemble *Triphyllopteris collombiana* as figured by Schimper (1862, pl. 25, figs. 8–10, *Cyclopteris*) from Burbach. The nervation is well shown in Pl. 26, fig. 42.

It is possible that the specimens figured as *Adiantites peruianus* and *A. bassleri* by Read (1938) belong to this species.

### ***Triphyllopteris lescuriana*** (Meek)

(Pl. 26, figs. 43–45)

The specimens referred to this species are much smaller and the leaves are more divided than in *Triphyllopteris collombiana*. In every case the pinnules are divided in a way which is typical for this genus.

The specimens represented in Pl. 26, figs. 43, 44, have elongated, acuminate divisions of the individual segments. Fig. 43 is part of the top of a leaf and shows the division of the segments very clearly. As far as can be seen the venation agrees with that described for *Triphyllopteris*.

It is very probable that the specimen figured in Pl. 26, fig. 45 also belongs to this species, although the divisions of the pinnules are not so sharply acuminated. Good examples of *Rhacopteris ovata* occur on this specimen, one with large, and one with small pinnules.

These specimens agree rather well with *Triphyllopteris lescuriana* (Meek) as figured by Jongmans, Gothan & Darrah (1937, pl. 44, figs. 7, 8) and by Lesquereux (1880, pl. 50, fig. 6).

### ? ***Triphyllopteris peruviana*** n. sp.

(Pl. 26, fig. 46)

DIAGNOSIS. Dimensions much smaller than in *T. lescuriana* and the division of the leaf much denser. Pinnules divided in five lobes, the top lobe elongate, the side lobes rounded and much shorter than in *T. lescuriana.*

DESCRIPTION. The third form is represented by one good specimen (Pl. 26, fig. 46) and one fragment. The dimensions are much smaller and the division of the leaf is much denser. The division of the pinnules into three lobes is not so regular. In most cases there are five lobes, the top lobe being elongate, the side lobes more rounded and much shorter. It is not certain that this specimen really belongs to *Triphyllopteris* and it is therefore provisionally named ? *Triphyllopteris peruviana.* More and better material is necessary before it can be attributed to this genus with certainty.

## CONCLUSION

The flora of Carhuamayo contains :

*Lepidodendropsis de voogdi* Jongmans.
*Lepidodendropsis* cf. *de voogdi* Jongmans.
*Lepidodendropsis steinmanni* Jongmans.
*Lepidodendropsis* cf. *steinmanni* Jongmans.
*Lepidodendropsis* sp.
*Cyclostigma pacifica* (Steinmann) Jongmans.
*Cyclostigma* cf. *pacifica* (Steinmann).
*Rhacopteris ovata* (McCoy).
*Rhacopteris* cf. *circularis* Walton.
*Triphyllopteris collombiana* (Schimper).
*Triphyllopteris lescuriana* (Meek).
? *Triphyllopteris peruviana* Jongmans.

It is clear that this flora, as was to be expected, is of Mississippian age.

## THE DISTRIBUTION OF *LEPIDODENDROPSIS*

It is clear that the age of the Peruvian Carboniferous floras is Mississippian, and this was the opinion of most of the earlier authors. Berry, however, accepted a Pennyslvanian age for Paracas, but it has since been proved, in particular by Gothan, that the determinations upon which Berry based his conclusion were not correct. The records described in this paper fully agree with a Mississippian age.

As previously stated the Peruvian flora is very similar to that of the Pocono in the United States. A number of species of *Lepidodendropsis* were described from the Pocono (Jongmans, Gothan & Darrah, 1937) some of which resemble the type species *Lepidodendropsis hirmeri* Lutz. Other species such as *L. vandergrachti* have quite a different habit and are more like *Sigillaria.* The fructification of this species is not a strobilus but, as in *Pinakodendron*, the spores are found at the base of small sporophylls on young twigs. A similar fructification is recorded for the Peruvian *Lepidodendropsis de voogdi* Jongmans. Other important elements of the Pocono flora are some species of *Triphyllopteris*. *Rhacopteris* was not present in the Pocono collections examined.

*Trochophyllum breviinternodium* (Arnold, 1933; renamed *Prolepidodendron*, Arnold, 1939, pl. 1, fig. 2) very much resembles *Lepidodendropsis*. The only difference is in the form of the leaves, with their broad, flattened, upper ends. It is possible that this species is in some way a transition with *Protolepidodendron* Krejci which is certainly related to *Lepidodendropsis* but distinguished by the leaves which in their upper parts are divided into two. If the leaves are not preserved, or the division of the leaves is not visible, it is almost impossible to distinguish the stems of *Protolepidodendron scharyanum*, as figured by several authors, from those of *Lepidodendropsis*.

Arnold's specimens are from the Upper Devonian (Oswayo sandstone), near Port Allegany, McKean County, Pennsylvania, which was originally placed in the Pocono (Arnold, 1933).

*Prolepidodendron breviinternodium* (Arnold) has been found associated with *Archaeopteris* cf. *roemeriana*, *Rhacopteris* sp. (cf. *R. circularis* Walton from the Teilia beds), and fragments of *Callixylon*.

*Colpodexylon* Banks (1944) is another related genus with dichotomous or three-forked leaves.

Lutz (1933) described *Lepidodendropsis* as a new genus from the Lower Carboniferous of Geigen near Hof, Bavaria. In that flora *L. hirmeri* is represented by an abundance of very good specimens. Other important elements in the flora are: *Sphenophyllum saxifragaefolioides* Leyh., *S. geigense* Lutz, *Neurocardiopteris*, *Cardiopteris*, *Rhacopteris lindsaeformis* Bunb., *R. semicircularis* Lutz, *Archaeopteridium dawsoni* Stur, *Sphenopteridium*, *Calathiops* and different species of *Rhodea*.

It is interesting to note that Lacey (1952 : 375,376) mentions two specimens from the Lower Carboniferous of Wales both of which may well belong to *Lepidodendropsis*. One of the specimens is from Craig Quarry, nr. Denbigh. The other (p. 375) comes from the Dyserth locality and was originally named *Lepidophloios* cf. *laricinus* Sternberg.

Dubertret (1933 : 288) has recorded lepidodendroid remains associated with a Tournaisian fauna in the Jebel Abd el Aziz, North-east Syria, and Mr. W. N. Edwards informs me that there are some fragments probably referable to *Lepidodendropsis* in the British Museum (Natural History) collected by W. A. Macfadyen from the Wadi Gharra, Jebel Abd el Aziz.

Another flora which may be compared with that of the Peruvian Lower Carboniferous was described from Egypt (Jongmans & Koopmans, 1940). It was collected from samples of cores from wells in Rhas Gharib. The flora contains *Lepidodendropsis fenestrata* J. & K., *Sphenopteris whitei* (Berry)—originally named *Rhodea* cf. *hochstetteri*; the new determination, not yet published, is based on better specimens collected in 1946—and *Cyclostigma aegyptiaca* J. & K.

In the same paper some specimens from Wadi Um Shebba, Sinai, were figured, which may also be compared with, and probably belong to *Lepidodendropsis* (*Lepi-*

*dodendropsis sinaica* J. & K. including two specimens of *Lepidodendron mosaicum* Salter figured by Seward, 1932, pl. 21, fig. 4, and pl. 22, fig. 9). In connection with the Carboniferous of Egypt it is interesting that *Porodendron* sp. described by Gothan (1933) from the Oasis di Cufra, may also belong to *Lepidodendropsis*.

An important contribution to the *Lepidodendropsis* flora of North Africa was published by Boureau (1954). He records the occurrence of *Rhacopteris ovata* and *R. circularis* in the Lower Carboniferous (? Dinantien) of Aïr, near Tafadeck, Central Sahara. Although *Lepidodendropsis* itself was not found at this locality, it is very probable that the horizon is that of the *Lepidodendropsis* flora, for according to a young French geologist whom I met in Algeria, he had collected *Lepidodendropsis* from the Lowest Carboniferous of the Sahara. I have not yet, however, seen the specimen which he promised to send to me for examination.

A plant which certainly belongs to *Lepidodendropsis* is *Sigillaria fezzanensis* Chiarugi (1948). This specimen is much like *Lepidodendropsis vandergrachti* J., G. & D. from the American Pocono and probably belongs to this species. It has nothing to do with *Sigillaria* and certainly not with *S. brardi* Bgt. with which it is compared by Chiarugi. On the strength of this comparison Chiarugi states that the locality belongs to an elevated part of the Carboniferous. In my opinion it belongs to the Lower Carboniferous or Upper Devonian in agreement with the marine fossils, which according to Borghi (1939) indicate a transition between the Mississippian and the Upper Devonian.

Chiarugi (1948 : 81) compares his material with Fritel's *Archaeosigillaria vanuxemi* Goepp. (1925, pl. 3, figs. 1–5). These specimens have leaf-cushions which are very approximate. However, fig. 3, upper part, and fig. 5 show clearly that the space between the individual leaf-cushions can become much larger. It is not clear from the figures whether there is a true leaf-scar, as in *Archaeosigillaria*, or not. A comparison of *Archaeosigillaria* and *Lepidosigillaria* with *Lepidodendropsis* can only be made by an examination of the original specimens.

Another figure in Fritel's paper with which comparison is possible is his *Lepidodendron* cf. *volkmannianum* (pl. 3, fig. 6*b*). This specimen was found at the same locality as his *Archaeosigillaria*.

Carpentier (1930) described a small flora from the Lower Carboniferous of Morocco. His *Lepidodendron ?* aff. *corrugatum* (pl. 1, fig. 3), Epi de Calamariée ? (pl. 2, fig. 3) and *Lepidodendron veltheimi* (pl. 4, figs. 1–3) most probably belong to *Lepidodendropsis*. It may even be that his *Arctodendron* (pl. 5, figs. 2, 2 bis) is an old stem of *Lepidodendropsis*. It is very curious, however, that at this locality, some very poorly preserved specimens were collected which simulate impressions of *Sigillaria*.

*Lepidodendropsis hirmeri* has also been collected by Meléndez and myself (1950) from the Lower Carboniferous of Valdeinfierno, Spain. Here it occurs at the same locality, but not exactly in the same place, with a flora containing *Asterocalamites scrobiculatus* Schl., *Stigmaria stellata* Goepp., *Sphenophyllum saxifragaefolioides* Leyh, *S. geigense* Lutz, *Rhodea* cf. *stachei* Stur, *R.* cf. *moravica* Ett., *Triphyllopteris* cf. *minor* J. & G., *T. collombiana* (Sch.), and *Calathiops* cf. *plauensis* Gothan.

This flora very much resembles that of Geigen, near Hof, and both may be compared with the floras of the Pocono, of Peru and of Egypt.

In the Donetz Basin the *Lepidodendropsis* flora is said to occur in the Upper Devonian. Zalessky (1931) described *Heleniella theodori* and compared it with some species of *Sigillaria* (*S. youngiana* Kidston, *S. tschirkovaeana* Zal., and *S. canobiana* Kidston) which show undulated ribs. However, an examination of well-preserved material collected by Zalessky and myself (1939) proved that they have nothing to do with *Sigillaria*. There are no ribs, but *Lepidodendron*-like leaf-cushions. The leaf-trace is never visible. These plants are identical with *Lepidodendropsis hirmeri* Lutz. Lutz compared *Lepidodendropsis* with *Helenia*, but the specimens of this latter genus, which occurs with *Heleniella*, are for the most part badly preserved. Undoubtedly most of the species of *Helenia* described by Zalessky (1931), especially *H. similis* and *H. bella*, belong to *Lepidodendropsis*. The same may be true for the specimens he calls *Lepidodendron stylicum*, but most of these are very intensively decorticated.

Zalessky (1930) described a new genus, *Micheevia*, from the Lower Carboniferous of the Ural mountains. Some of the species are indeterminable but *M. rimnensis*, *M. pulchella* and *M. uralica* certainly belong to *Lepidodendropsis*. M. *uralica* can be compared with *L. vandergrachti* from the Pocono, and *M. pulchella* with *L. hirmeri*.

In the same paper he figures *Helenia inopinata* which also belongs to *Lepidodendropsis*. The same may be said for his *Lepidodendron glincanum* (pl. 2, figs. 3, 4), but the specimens, some of which show their internal structure, are too decorticated to be certain. Possibly *Lepidodendron caracubense* Zalessky (1921) ought to be included in *Lepidodendropsis* but this is not certain.

It is probable that the specimen described by Schmalhausen (1883) as *Lepidodendron glincanum* Eichw. from the Egorshino region, together with those identified by Mägdefrau (1936, pl. 10, figs. 6–8) as *Heleniella theodori* from the Upper Devonian in the Thüringer Wald, and Gilkinet's *Lepidodendron nothum* (1922, pl. 13, fig. 76), all belong to *Lepidodendropsis*.

Gothan & Zimmermann (1937) described lepidodendroid remains from the Upper Devonian of Bögendorf-Libichau near Waldenburg. Several of their figures are very much like *Lepidodendropsis* but in most cases the specimens are too incomplete or too badly preserved to be certain. The small stems (pl. 24, figs. 1–4) and the specimens ascribed to *Protolepidodendropsis frickei* G. & Z. (pl. 24, figs. 6*a*, *b* ; pl.25, figs. 1, 1*a*, ? 7) almost certainly belong to *Lepidodendropsis*. In my opinion there is no reason for the creation of a new genus for these stems. Whether they are specifically identical with any of the species described in *Lepidodendropsis* is another question. However, there is a resemblance to *L. hirmeri* Lutz. Kräusel & Weyland (1949 : 136) also state that this genus is practically indistinguishable from *Lepidodendropsis*.

Gothan & Zimmermann (1937, pl. 22, figs. 1–4) described and figured a new species of *Sublepidodendron* (*S. antecedens*) from the Upper Devonian of Oberkunzendorf. Kräusel & Weyland (1949 : 146) state that it can be compared with *Lepidodendropsis*. It very probably belongs to this genus.

Hoeg (1942) described a new species of *Protolepidodendropsis* (*P. pulchra* Hoeg) from the Upper Devonian of Mimerdalen, Spitsbergen. He compares it with *Heleniella theodori* Zal. from the Donetz Basin, with *Protolepidodendron*, and with

*Protolepidodendropsis frickei*. Most of the specimens figured by Hoeg in his pls. 54 and 55 cannot be separated from *Lepidodendropsis*.

Another group of lepidodendroid plants with which Hoeg compares his new species is *Sublepidodendron*, especially *S. subfallax* Nath. and *S. nordenskioldi* Nathorst (1920). Several of Nathorst's figures resemble *Lepidodendropsis* at first sight, but the structure and position of the leaf-cushions in *Sublepidodendron* do not permit one to unite them with *Lepidodendropsis*. The most typical species described by Nathorst from Spitsbergen, *Sublepidodendron mirabile*, *S. fallax*, *S. subfallax* and *S. nordenskioldi*, are considered by Gothan (1933) to be synonymous, and he includes them all in one species *Sublepidodendron mirabile* Nathorst. Gothan, however, does not use this generic name and retains the species under *Lepidodendron*. In my opinion and in accordance with Nathorst (1920), Hirmer (1927) and Gothan & Zimmermann (1937) it is necessary to separate them from *Lepidodendron*. Gothan also unites *Lepidodendron leeianum* G. & S. with *L. mirabile*, but Sze (1936) does not agree and considers the former to be a distinct species of *Sublepidodendron*.

Possibly *Lepidodendron calamitoides* Nathorst (1920, pl. 5, figs. 1–8, ? 9) also belongs to this group. The relationship of *L. kidstoni* Nathorst (1920, pl. 3, figs. 1*a*, 2–7) is more doubtful. It may be that such specimens are in some respects already transitional to the true Lepidodendra. There are several species of *Lepidodendron* in the Namurian and in the upper part of the Mississippian, which resemble *Sublepidodendron* in many characters, but their leaf-cushions, and especially their true leaf-scars, are lepidodendroid. Such species include *L. kidstoni* Nath. (which can be compared with *Sublepidodendron*), *L. robertii* Nath., *L. acuminatum* Goepp., *L. spetsbergense* Nath., *L. osbornei* Walkom and perhaps *L. volkmannianum*.

Carpentier (1932 : 33) compared the previously described *Lepidodendron corrugatum* Dawson (Carpentier, 1925, pl. 13, figs. 6–8) from the Tournaisian of Bois Gamats, near Laval (Mayenne), with *Heleniella theodori* Zal. So far as one can judge from his figures, especially that of 1932, he is quite right in this comparison, and in my opinion they are at least distantly related to *Lepidodendropsis hirmeri*. Zalessky (in litt.) objected to Carpentier's conclusions and supposed that the French specimens most probably belonged to a new type. His objections, however, were based on incomplete knowledge of his genus *Heleniella*. A revision of this genus has since been made, based on new material collected by Zalessky and myself.

*Lepidodendropsis* is also known from some other localities in Asia. Zalessky (1937) figures a small poorly preserved specimen from the River Niaysse, 4 km. from the River Mania-Niaysse, which he names *Heleniella theodori*. It may belong to *Lepidodendropsis* but it is impossible to be certain. From the same locality he describes *Ularia ovalis* Zal. which he considers to be a rhizome of a Lepidophyte (Zalessky, 1937 : 10, pl. 9, fig. 1). It is possible that this also is a fragment of *Lepidodendropsis*. He compares the specimen with *Stigmaria exigua* Dawson (1871, pl. 3, fig. 30, 30*a*) but Dawson's specimen does not allow further determination.

As already mentioned Sze (1936) does not agree with Gothan's identification of *Lepidodendron leeianum* Gothan & Sze with *Sublepidodendron mirabile* Nath. In the same paper Sze describes a number of specimens from the Chinese province of

Kiangsu as *Lepidodendron* aff. *leeianum* Goth. & Sze (? n. sp.) which very much resemble *Lepidodendropsis*. He states that the leaf-scars are not very distinct. In the figures, especially pl. 2, fig. 2, the leaf-cushions are very similar to those of *Lepidodendropsis*, and no leaf-scar is present.

*Protolepidodendron* (?) *arborescens* Sze (1936*a*) almost certainly belongs to *Lepidodendropsis*. It has nothing to do with *Protolepidodendron*, which is characterized by leaves divided in their upper parts. Sze (pl. 2, fig. 8) figures a divided leaf, but there is no proof that it belongs to this species. He compares the species with *P. scharyanum* Krejci (Halle 1936, pls. 2, 3; text-fig. 1) from Yunnan, which, apart from the division of the leaves, is also much like *Lepidodendropsis*. I should not hesitate, if such leaves were absent, to unite it with this genus.

Halle's material shows that at least some of the specimens named *Protolepidodendron* are distinguishable from *Lepidodendropsis* by the divided leaves only. Whether the presence or absence of the division in these leaves is sufficient ground for a generic separation (cf. Kräusel & Weyland 1949 : 136) is, in my opinion, rather doubtful. Sze also doubts whether such specimens as those figured by Halle belong to *Protolepidodendron*.

Walkom (1928) described two new species of *Protolepidodendron* (*P. lineare* and *P. yalwalense*) from Yalwal, New South Wales. He compared the first with *P. primaevum* (White) which has since been named *Lepidosigillaria* (Kräusel & Weyland, 1949 : 148), and *P. yalwalense* with *Lepidodendron karakubense* Schmalh. which is possibly *Lepidodendropsis*. Both the plants used for comparison by Walkom have been recorded from beds considered to be Upper Devonian, and for this reason Walkom also includes the Yalwal beds in the Upper Devonian, although they are considered to be Carboniferous by Clarke and other authors.

At a number of localities the flora, as far as it is known, does not contain *Lepidodendropsis*, but *Rhacopteris* of the *ovata* group only. Such is the case in Australia (Feistmantel 1890), some parts of South America, and also in Spiti, India, the flora of which has been described by Gothan & Sahni (1937).

It is clear that the *Lepidodendropsis* (*Rhacopteris*) flora, or at least related floras, are found all over the world, and this is very important for the stratigraphy of the Lower Carboniferous and for comparison with the Upper Devonian. It is interesting to note that such plants, especially *Lepidodendropsis*, also occur in different localities which are considered as Upper Devonian. This fact is not surprising, since in many cases it is almost impossible to separate what is considered to be Upper Devonian from the Lower Carboniferous. In some cases these so-called Upper Devonian floras are typical *Lepidodendropsis* floras, as in the Donetz Basin.

It is possible that the *Lepidodendropsis-Rhacopteris* floras represent a transition between the *Archaeopteris-Cyclostigma* floras of the Devonian and the floras of the lower part of the Mississippian.

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## EXPLANATION OF PLATES

The specimens figured in Pl. 17–20 are in the Department of Geology, British Museum (Natural History). Those figured in Pls. 21–26 belong to the Geologisch Bureau, Heerlen. All the photographs were taken by Mr. Van Voskuijlen, Geologisch Bureau, Heerlen.

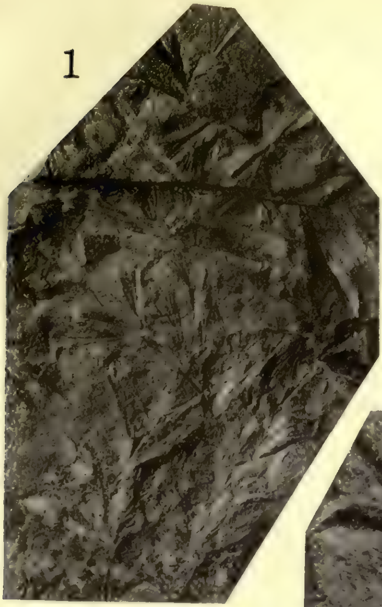
Unless otherwise stated all the figures are natural size.

### PLATE 17

### *Sphenopteris whitei* (Berry) and *Cyclostigma pacifica* (Steinmann).
### Lower Carboniferous (Mississippian); Paracas, Peru.

Fig. 1. *Sphenopteris whitei* (Berry). V.25936.
Fig. 2. *Sphenopteris whitei* (Berry). Counterpart of fig. 1. V.25936*a*.
Fig. 3. *Sphenopteris whitei* (Berry). V.25942.
Fig. 4. *Sphenopteris whitei* (Berry). Part of counterpart of fig. 1. V.25936*b*.
Fig. 4*a* Enlargement of fig. 4, × 3.
Fig. 5. *Cyclostigma pacifica* (Steinmann). V.25925.
Fig. 5*a* Enlargement of fig. 5, × 3.
Fig. 6. *Cyclostigma pacifica* (Steinmann). V.25925*a*.
Fig. 6*a* Enlargement of fig. 6, × 3.
Fig. 7. *Cyclostigma pacifica* (Steinmann). V.25928.

1



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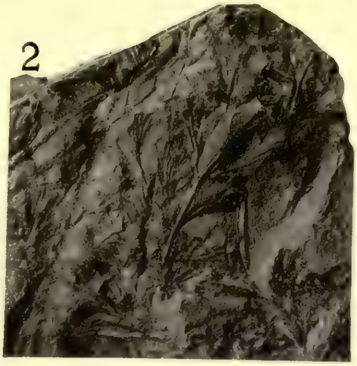

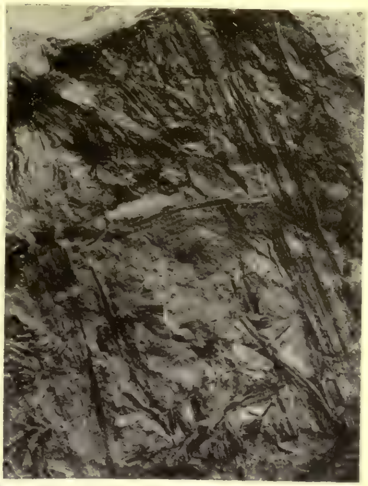

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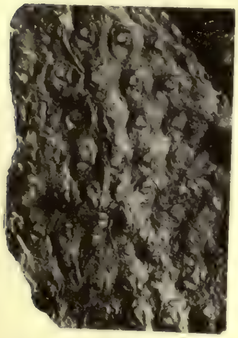

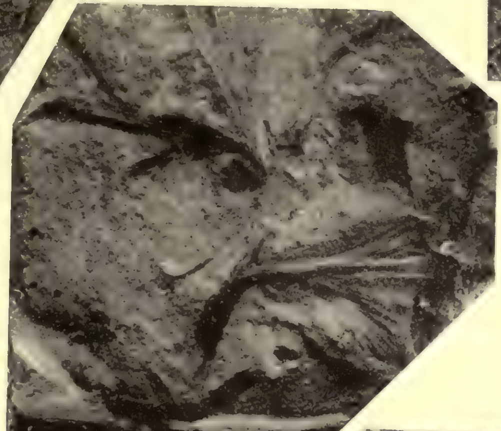

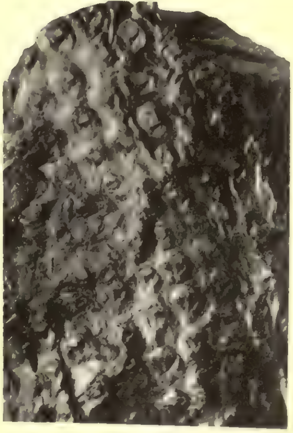

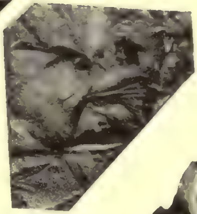

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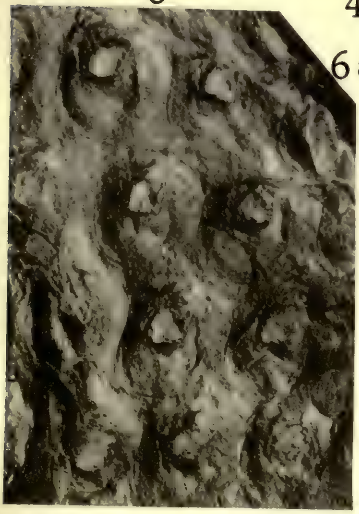

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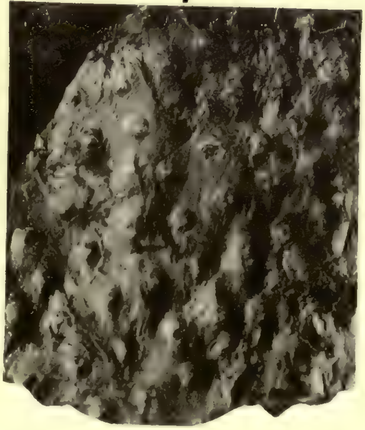
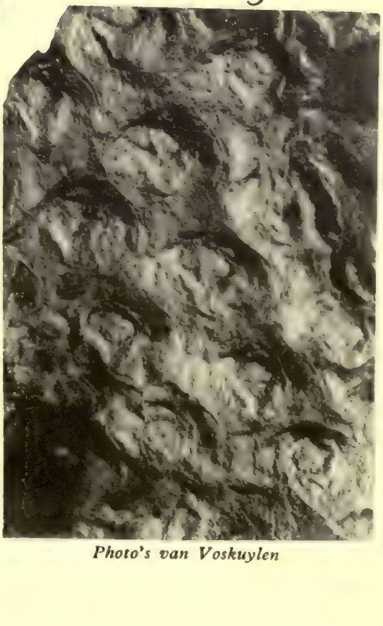
5a





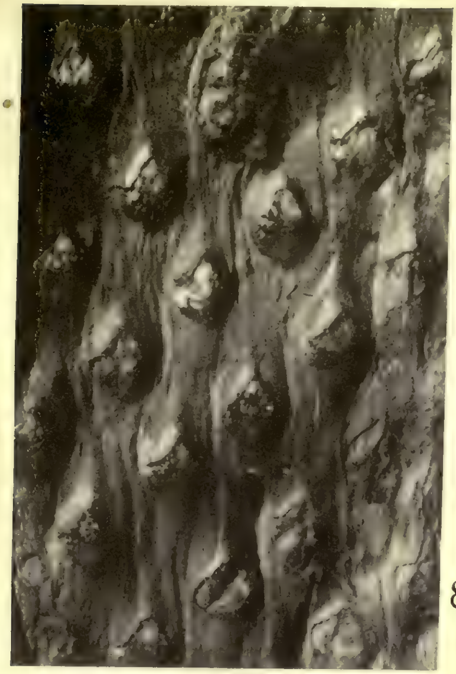
*Photo's van Voskuylen*

SPHENOPTERIS, CYCLOSTIGMA

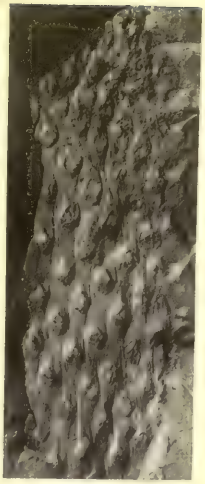
# PLATE 18

*Cyclostigma pacifica* (Steinmann).
Lower Carboniferous (Mississippian) ; Paracas, Peru.

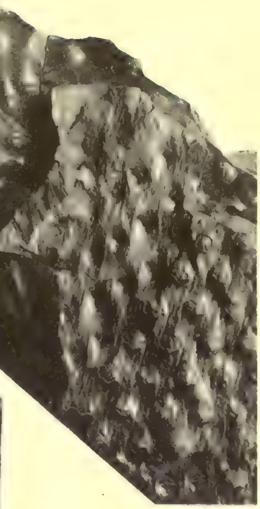
FIG. 8. *Cyclostigma pacifica* (Steinmann). V.25920.
FIG. 8*a* Enlargement of fig. 8, × 3.
FIG. 9. *Cyclostigma pacifica* (Steinmann). V.25918.
FIG. 9*a* Enlargement of fig. 9, × 3.
FIG. 10. *Cyclostigma pacifica* (Steinmann). V.25918*a*.
FIG. 10*a* Enlargement of fig. 10, × 3.



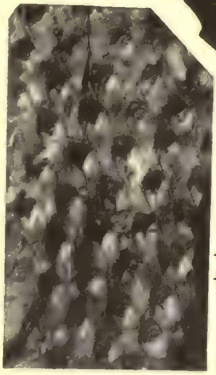
8 a



8



9



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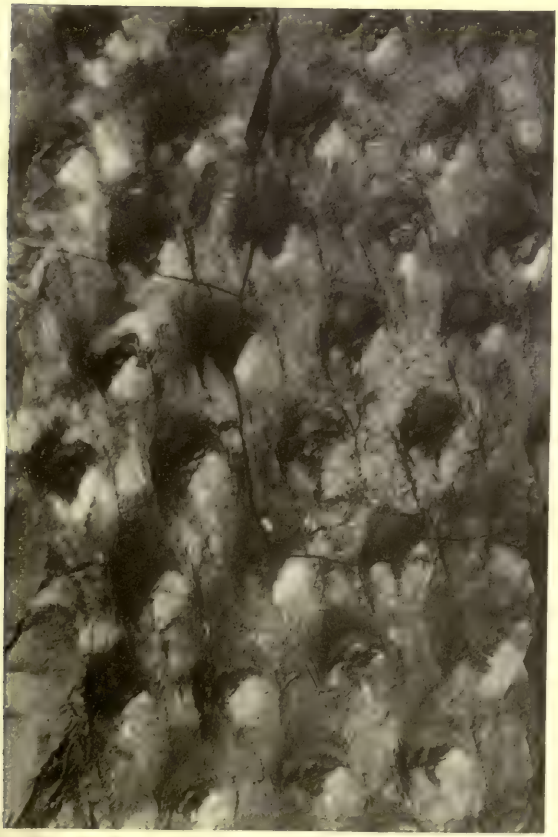
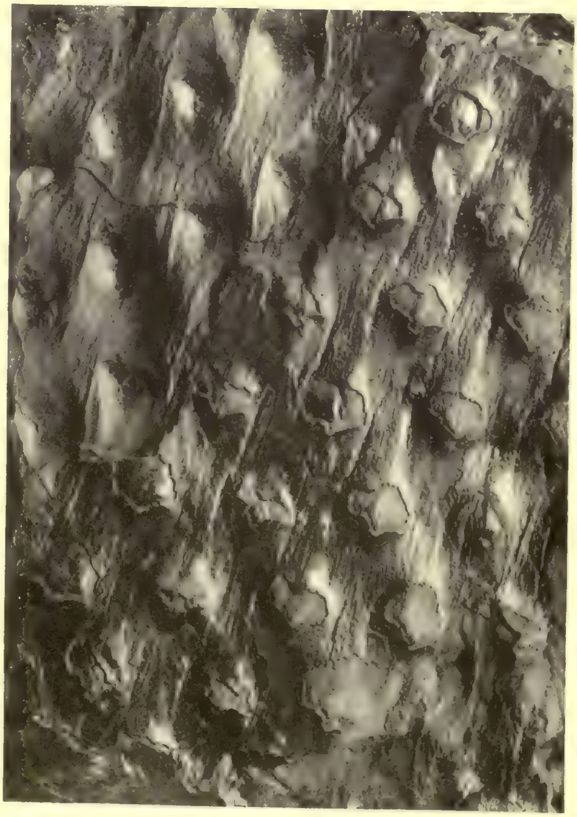


10 a



9 a

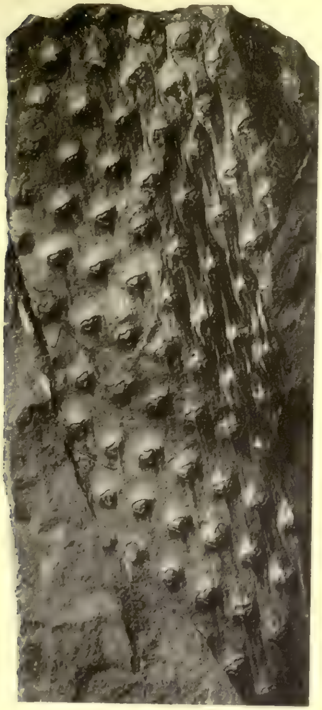
CYCLOSTIGMA

## PLATE 19

*Cyclostigma pacifica* (Steinmann).

Lower Carboniferous (Mississippian) ; Paracas, Peru.

FIG. 11. *Cyclostigma pacifica* (Steinmann). V.25917.
FIG. 12. *Cyclostigma pacifica* var. *decorata* Jongmans. V.25948.
FIG. 12*a* Enlargement of fig. 12, × 3.
FIG. 13. *Cyclostigma pacifica* (Steinmann). V.25933.
FIG. 14. *Cyclostigma pacifica* var. *decorata* Jongmans. V.25919.
FIG. 14*a* Enlargement of fig. 14, × 3.
FIG. $14b_1$ *Cyclostigma pacifica* (Steinmann). V.25916. Enlargements (figs. $14b_2$ and $14b_3$) on Pl. 20.



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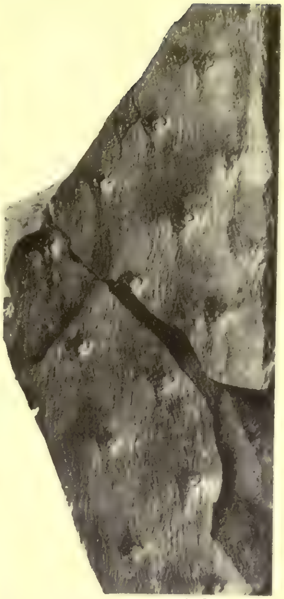

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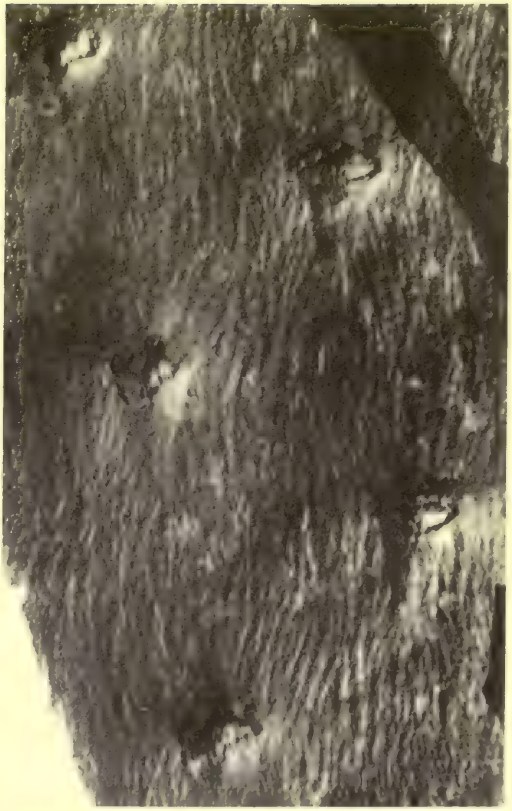

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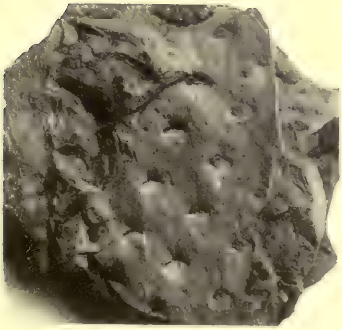

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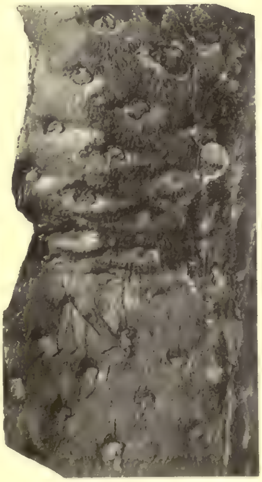

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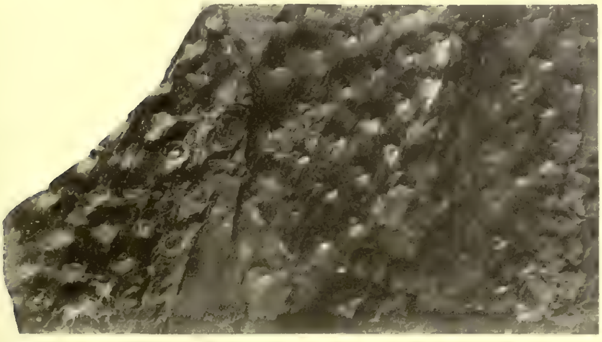
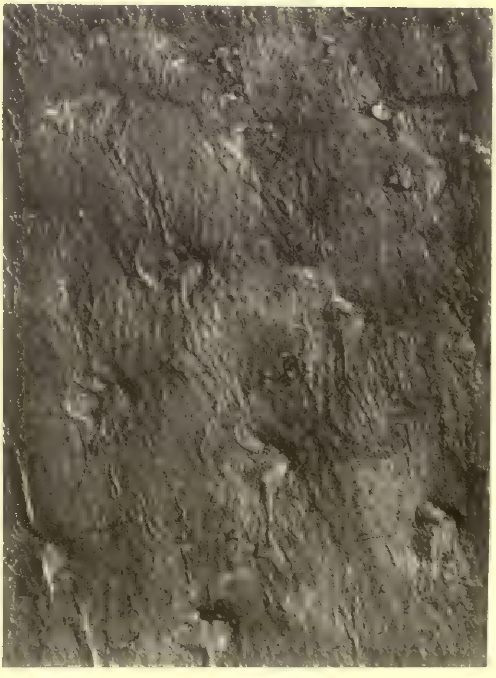


14b 1



14a

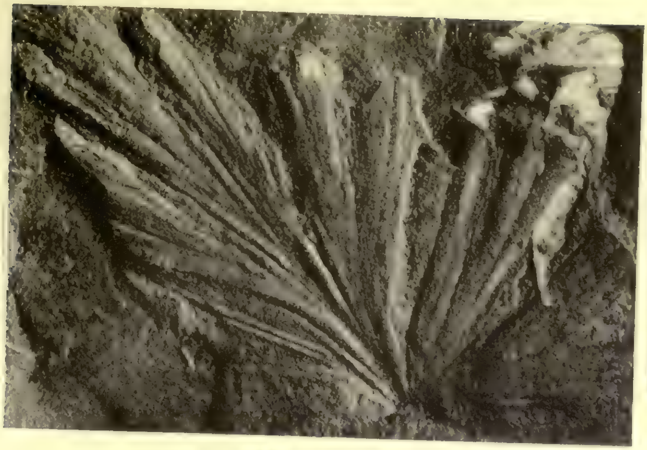
CYCLOSTIGMA

## PLATE 20

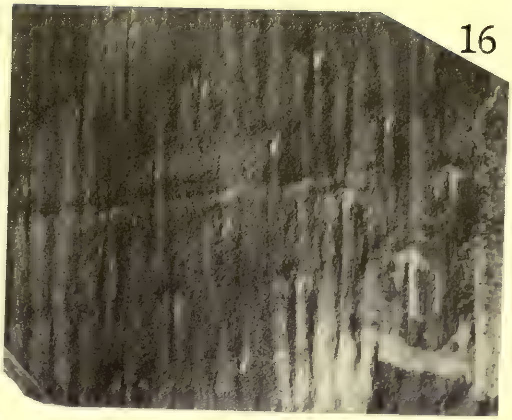
*Cyclostigma pacifica* (Steinmann), *Lepidodendropsis peruviana* (Gothan),
? *Lepidodendropsis lissoni* (Steinmann), *Lepidodendropsis* sp., *Rhacopteris* cf. *cuneata*
(Walkom) and *Rhacopteris ovata* (McCoy).

Lower Carboniferous (Mississippian) ; Paracas, Peru.

FIG. $14b_2$ *Cyclostigma pacifica* (Steinmann). Enlargement of fig. $14b_1$, × 3.
FIG. $14b_3$ *Cyclostigma pacifica* (Steinmann). × 3.
FIG. 15. *Lepidodendropsis peruviana* (Gothan). V.25911.
FIG. 16. ? *Lepidodendropsis* (*Lepidodendron*) *lissoni* (Steinmann). V.25932.
FIG. 17. ? *Lepidodendropsis* sp. V.25915.
FIG. 18. *Rhacopteris* cf. *cuneata* (Walkom). V.25948*a*.
FIG. 18*a* *Rhacopteris* cf. *cuneata* (Walkom) and *Rhacopteris ovata* (McCoy). The specimen is on the reverse side of that shown in fig. 12.
FIG. $18a_1$ *Rhacopteris* cf. *cuneata* (Walkom). Enlargement of fig. 18*a*, × 3.



18 a 1



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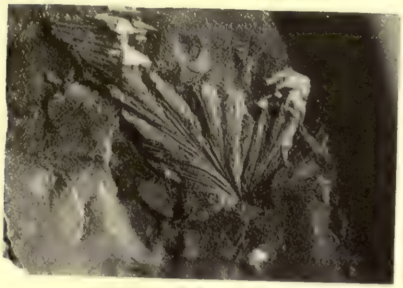
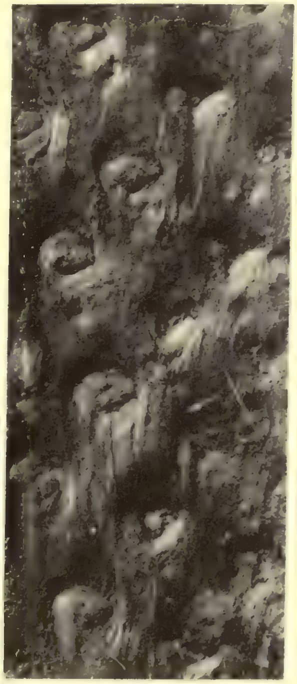
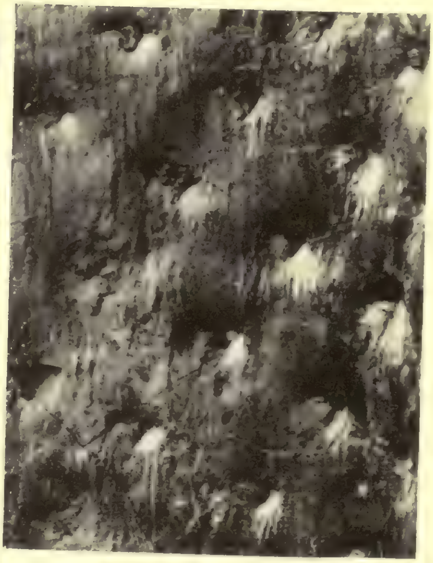


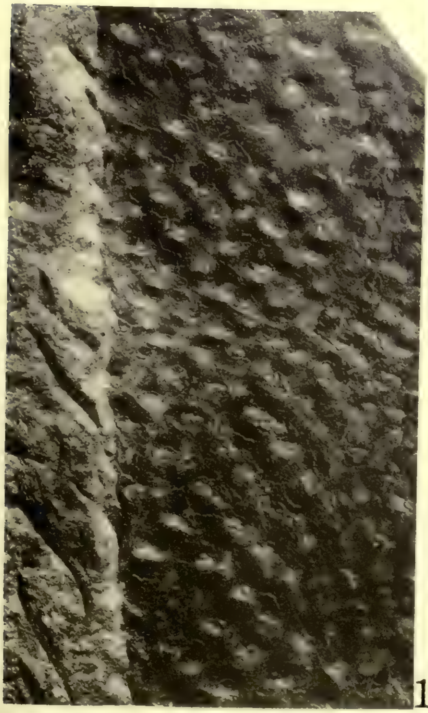
18 a



14 b 2



14 b 3



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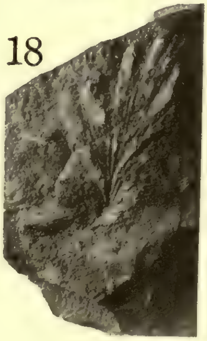

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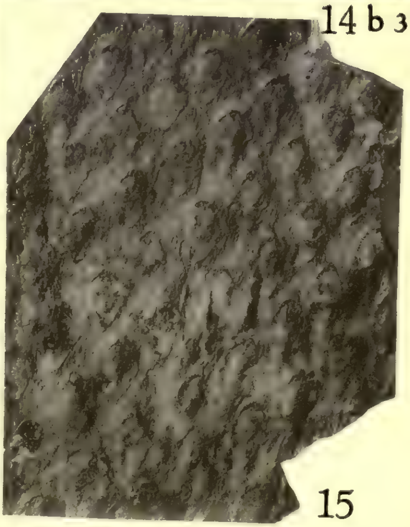


15

CYCLOSTIGMA, LEPIDODENDROPSIS, RHACOPTERIS

## PLATE 21

### *Lepidodendropsis de voogdi* n. sp.

### Lower Carboniferous (Mississippian) ; Carhuamayo, Peru.

FIG. 19. *Lepidodendropsis de voogdi* Jongmans. Photo 8414.

FIG. 20. *Lepidodendropsis de voogdi* Jongmans. Traces of the sporangia are visible on the left of the figure. Photo 8416.

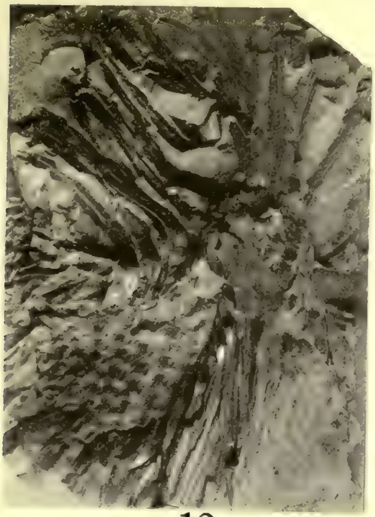
FIG. 21. *Lepidodendropsis de voogdi* Jongmans. Photo 8444.

FIG. 21*a* Enlargement of fig. 21, × 3.

FIG. 22. *Lepidodendropsis de voogdi* Jongmans, showing sporangia containing megaspores. Photo 8413.

FIG. 22*a* Enlargement of fig. 22, × 3.

FIG. 23. *Lepidodendropsis de voogdi* Jongmans. Photo 8413*a*.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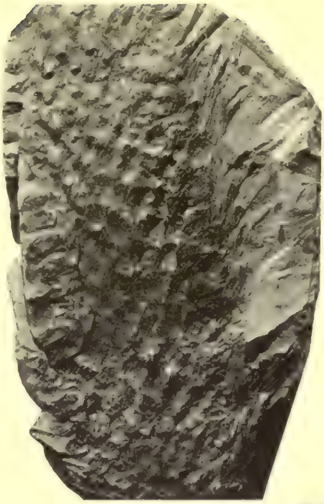
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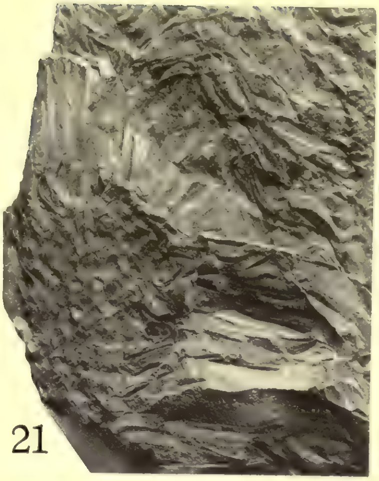
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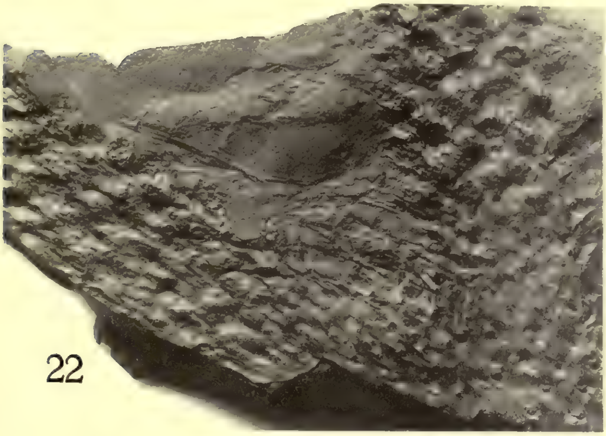
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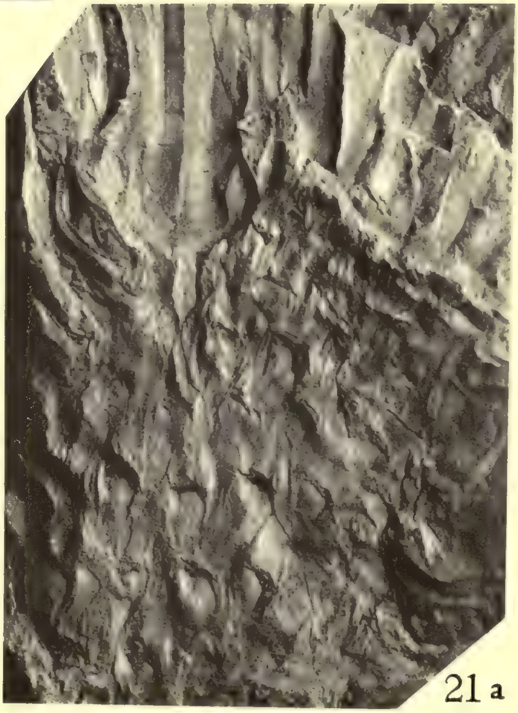
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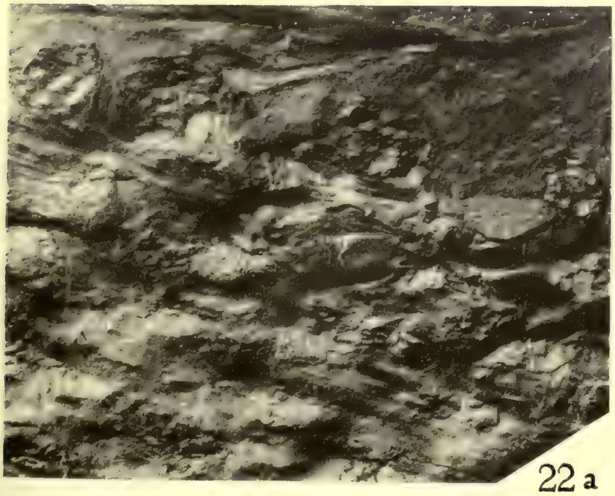
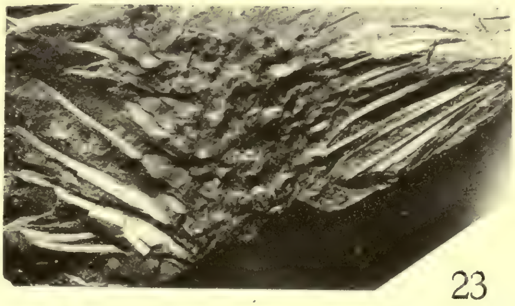

22 a


23

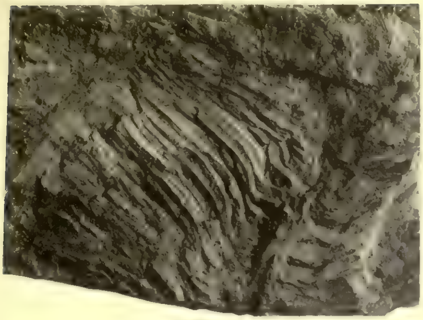
LEPIDODENDROPSIS

## PLATE 22

### *Lepidodendropsis de voogdi* n. sp., and *Lepidodendropsis steinmanni* n. sp.

Lower Carboniferous (Mississippian) ; Carhuamayo, Peru.

FIG. 24. *Lepidodendropsis de voogdi* Jongmans. Photo 8445.
FIG. 25. *Lepidodendropsis de voogdi* Jongmans. Photo 8449.
FIG. 26. *Lepidodendropsis de voogdi* Jongmans. Photo 8443.
FIG. 27. *Lepidodendropsis de voogdi* Jongmans. Photo 8448.
FIG. 28*a* *Lepidodendropsis steinmanni* Jongmans, showing habit of the stem with leaves. Photo 8415.
FIGS. 28*d*, 28*da*. Pith-cast, belonging to specimens in figs. 28*a* and 28*b* (Pl. 23). Photo 8450. Fig. 28*da*, × 3.



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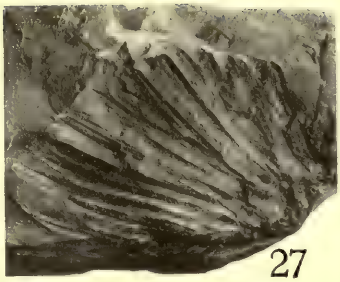

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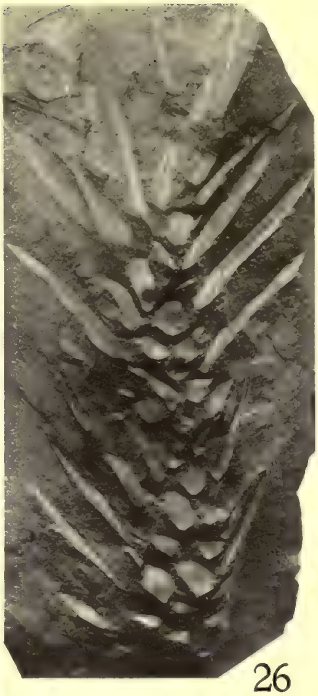

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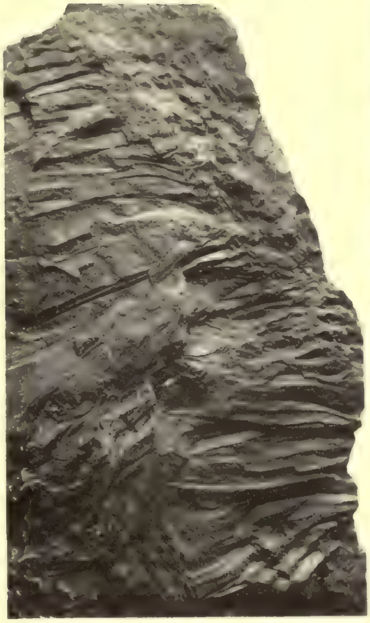

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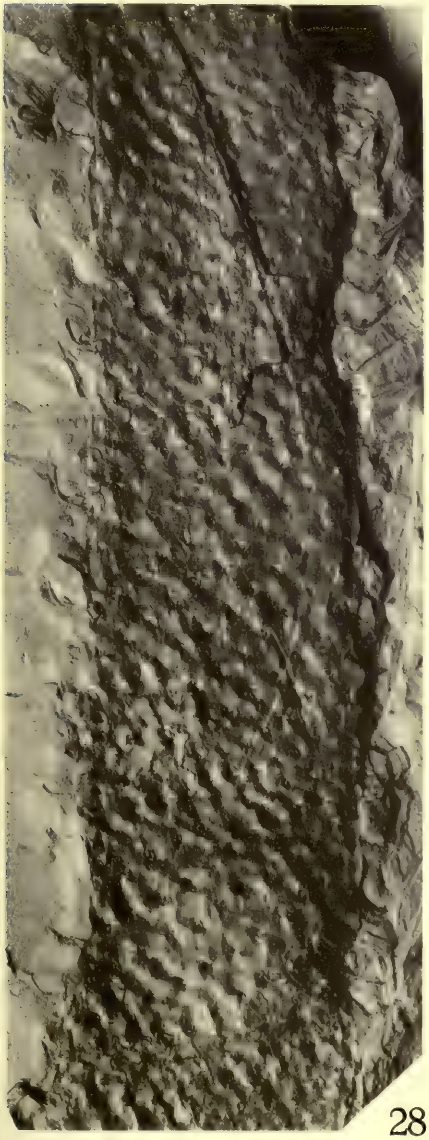
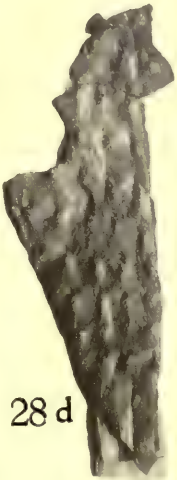
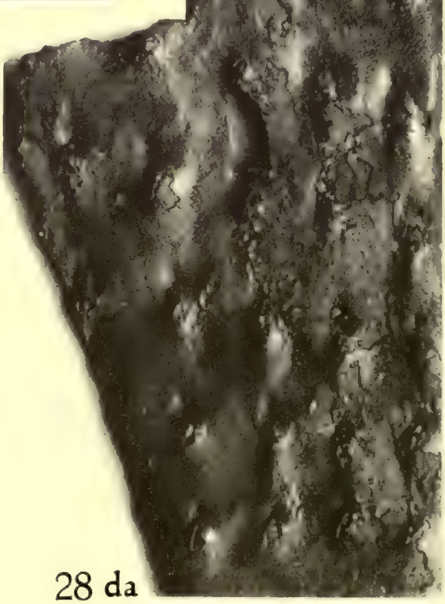


28 a



28 d



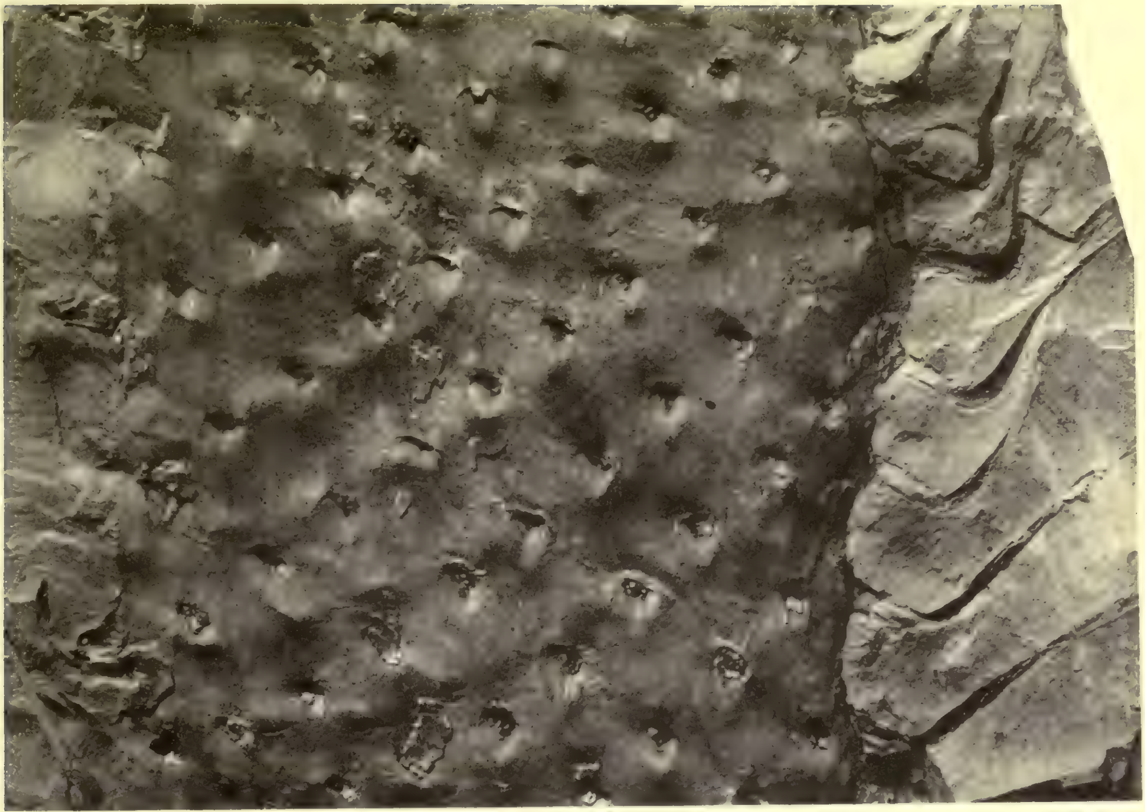
28 da

LEPIDODENDROPSIS

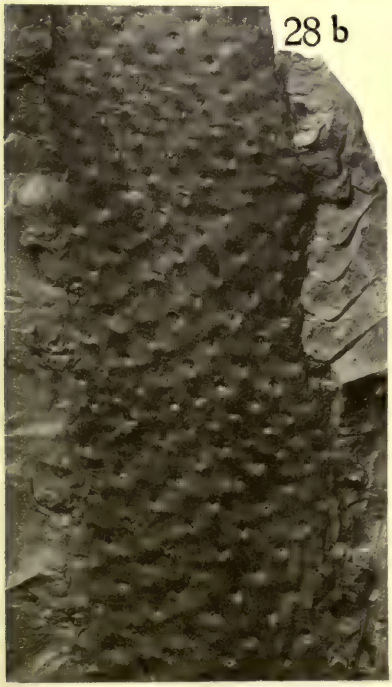
## PLATE 23

*Lepidodendropsis steinmanni* n. sp. and *Cyclostigma* cf. *pacifica* (Steinmann) var.
Lower Carboniferous (Mississippian); Carhuamayo, Peru.

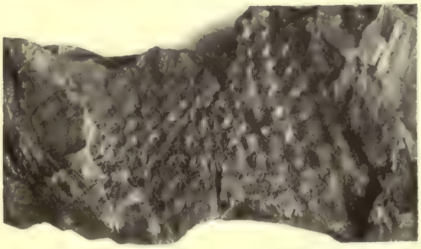
FIG. 28*b* *Lepidodendropsis steinmanni* Jongmans. Counterpart of fig. 28*a* with better preserved leaves. Photo 8415.
FIG. 28*c* Enlargement of part of Fig. 28*b* showing the leaves, × 3. Photo 8415.
FIG. 29*a* *Cyclostigma* cf. *pacifica* (Steinmann) var. Upper surface of stem. Photo 8451.
FIG. 29*aa* Enlargement of fig. 29*a*, × 3.



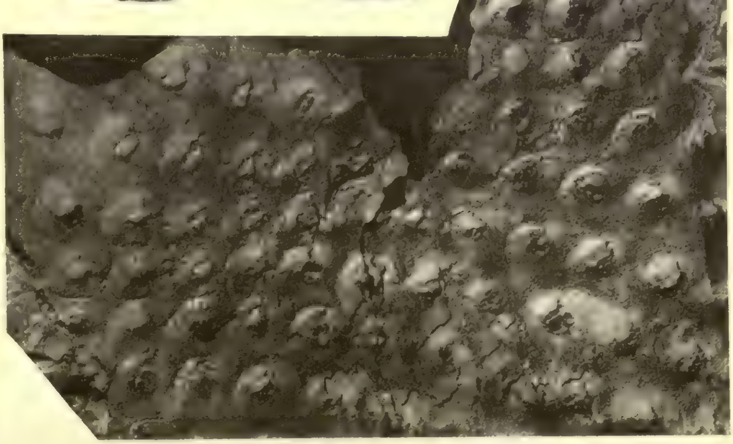
28 c



28 b



29 a



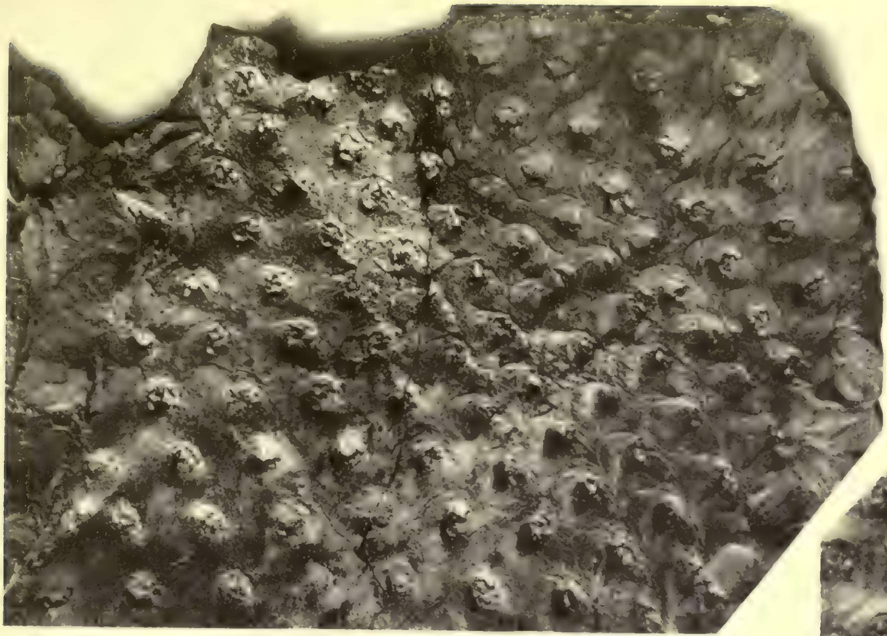
29 aa

LEPIDODENDROPSIS, CYCLOSTIGMA

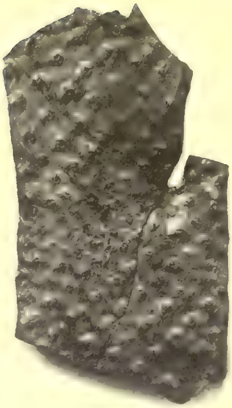
## PLATE 24

*Cyclostigma pacifica* (Steinmann) and *Lepidodendropsis* cf. *steinmanni* Jongmans.
Lower Carboniferous (Mississippian); Carhuamayo, Peru.

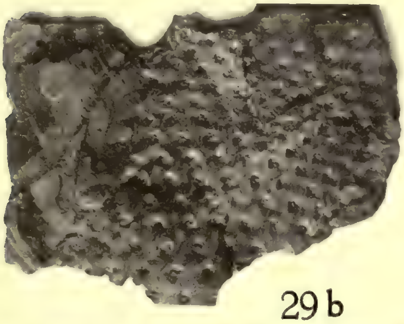
FIG. 29*b* *Cyclostigma* cf. *pacifica* (Steinmann) var. Lower surface of stem. Photo 8451.
FIG. 29*ba* Enlargement of fig. 29*b*, × 3.
FIG. 29*c* *Cyclostigma* cf. *pacifica* (Steinmann) var. Pith-cast belonging to figs. 29*a* and 29*b*. Photo 8451.
FIG. 29*ca* Enlargement of fig. 29*c*, × 3.
FIG. 30. *Cyclostigma pacifica* (Steinmann). With leaves attached. Photo 8532.
FIG. 30*a* Enlargement of fig. 30, × 3.
FIG. 31. *Lepidodendropsis* cf. *steinmanni* Jongmans. Photo 8447.



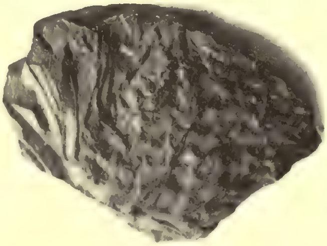
29 ba



29 c



29 b



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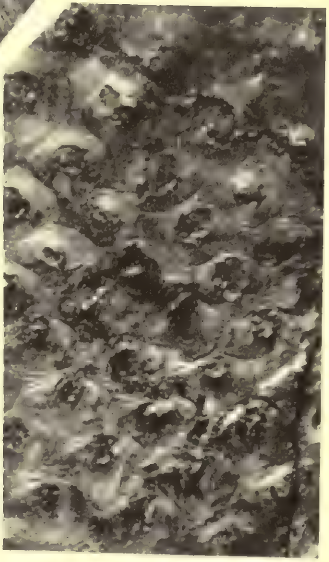
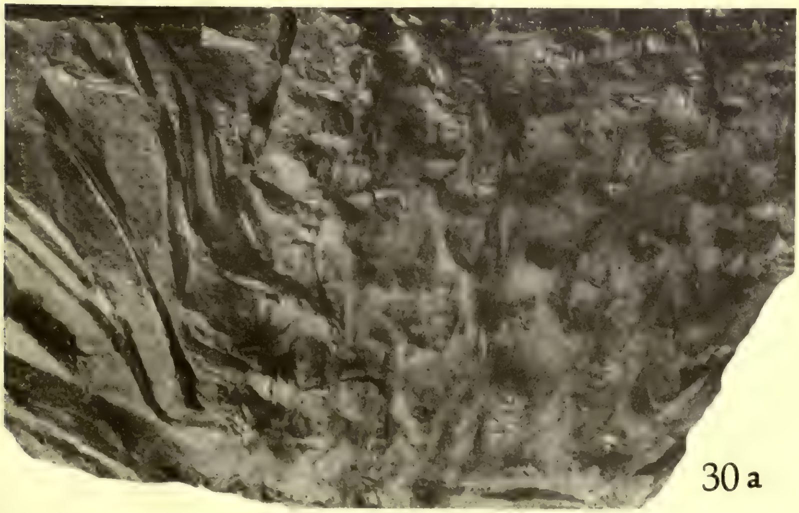
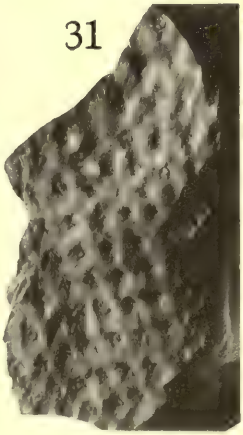


29 ca



30 a

31



CYCLOSTIGMA, LEPIDODENDROPSIS

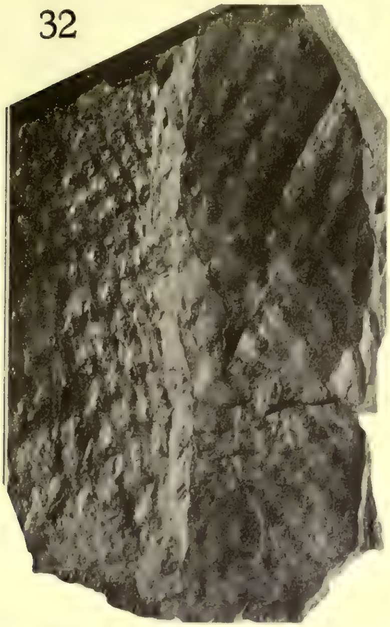
## PLATE 25

*Lepidodendropsis* cf. *de voogdi* Jongmans, *Rhacopteris ovata* (McCoy) and *Rhacopteris* cf. *circularis* Walton.

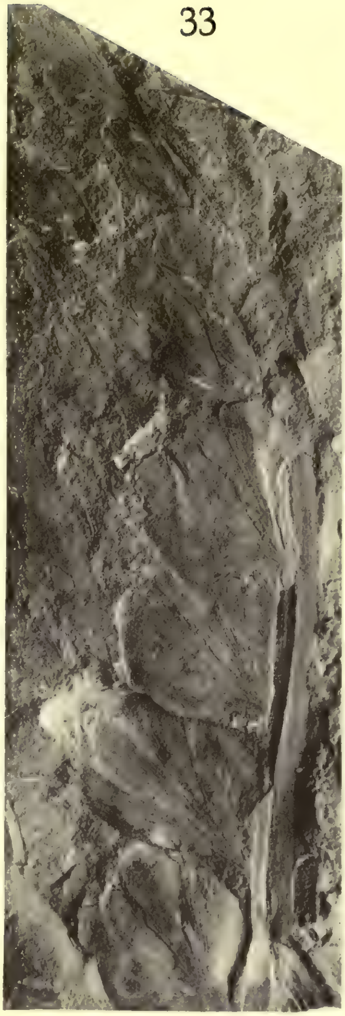
Lower Carboniferous (Mississippian) ; Carhuamayo, Peru.

FIG. 32. ? *Lepidodendropsis* cf. *de voogdi* Jongmans. Photo 8446.
FIG. 33. *Rhacopteris ovata* (McCoy). Photo 8456*d*.
FIG. 34. *Rhacopteris ovata* (McCoy). Photo 8456*b*.
FIG. 35. *Rhacopteris ovata* (McCoy). Photo 8452.
FIG. 36. *Rhacopteris ovata* (McCoy). Photo 8454.
FIG. 37. *Rhacopteris ovata* (McCoy). Photo 8453.
FIG. 38. *Rhacopteris* cf. *circularis* Walton. Photo 8456*a*.

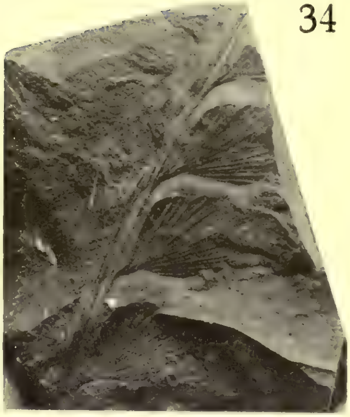
32



33



34



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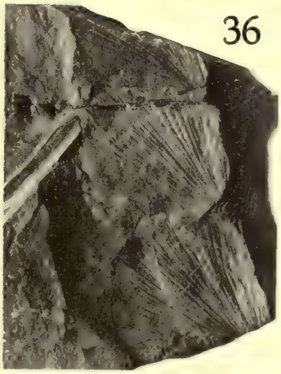

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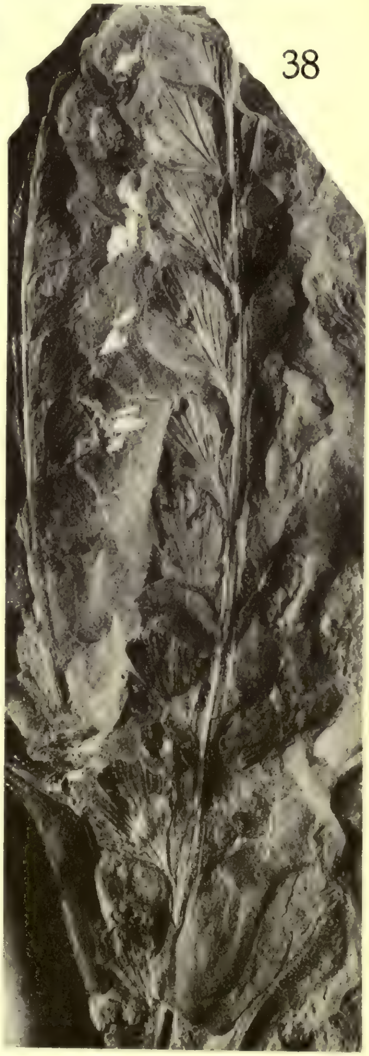
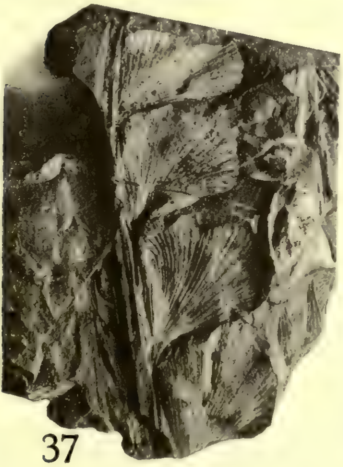
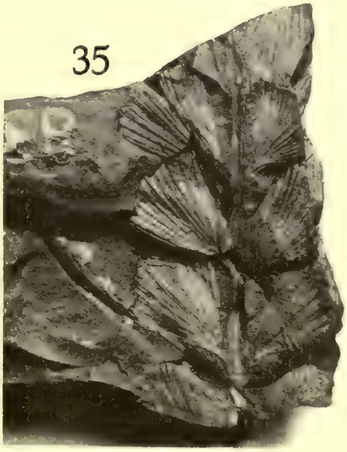




37

35



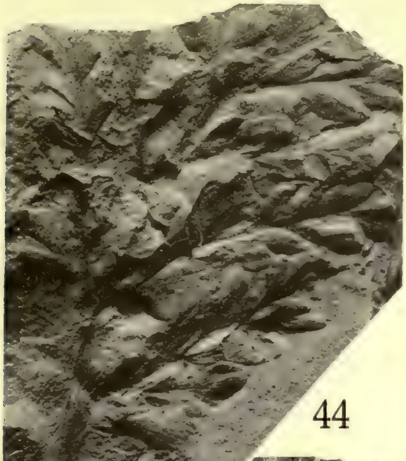
LEPIDODENDROPSIS, RHACOPTERIS

## PLATE 26

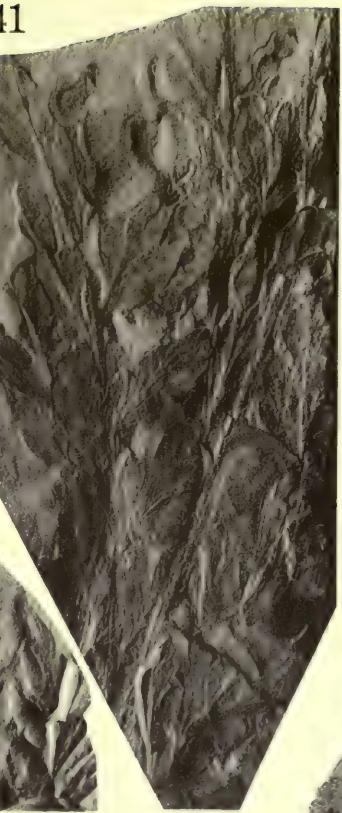
*Rhacopteris* cf. *circularis* Walton, *Rhacopteris ovata* (McCoy), *Triphyllopteris collombiana* (Sch.), *Triphyllopteris lescuriana* (Meek) and ? *Triphyllopteris peruviana* Jongmans.

Lower Carboniferous (Mississippian) ; Carhuamayo, Peru.

FIG. 39. *Rhacopteris* cf. *circularis* Walton. Photo 8456*c*.
FIG. 40. *Triphyllopteris collombiana* (Sch.) Photo 8455.
FIG. 41. *Triphyllopteris collombiana* (Sch.) Photo 8455*a*.
FIG. 42. *Triphyllopteris collombiana* (Sch.) Photo 8455*b*.
FIG. 43. *Triphyllopteris lescuriana* (Meek). Photo 8458*a*.
FIG. 44. *Triphyllopteris lescuriana* (Meek). Photo 8458*b*.
FIG. 45. *Triphyllopteris lescuriana* (Meek) and *Rhacopteris ovata* (McCoy). Photo 8458.
FIG. 46. ? *Triphyllopteris peruviana* Jongmans. Photo 8457.



44



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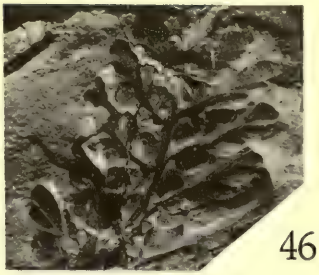

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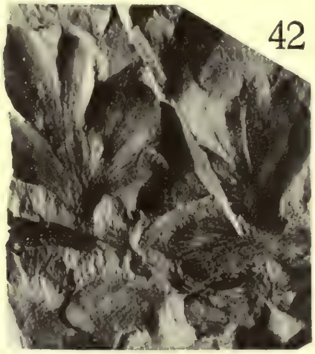

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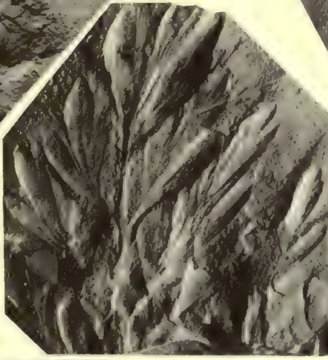

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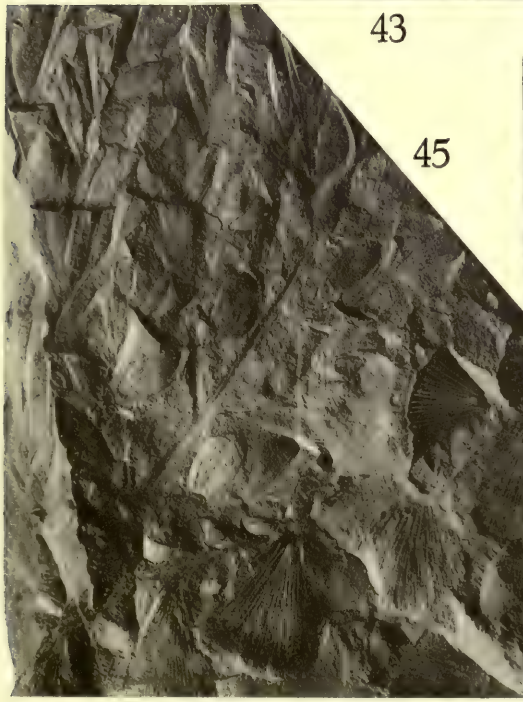

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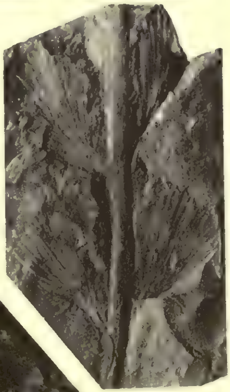

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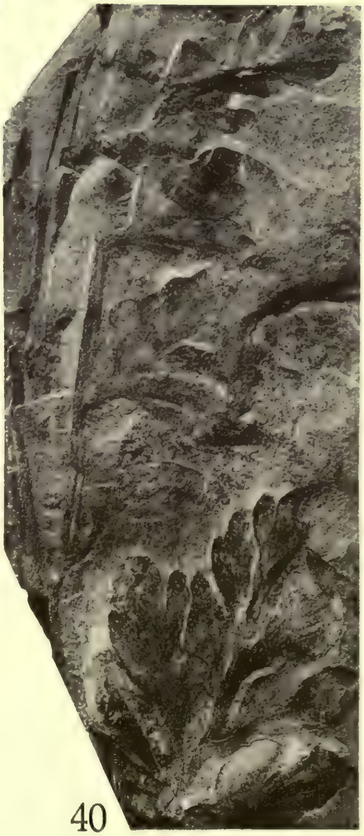

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# FURTHER CONTRIBUTIONS TO THE SOLUTION OF THE PILTDOWN PROBLEM

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# FURTHER CONTRIBUTIONS TO THE SOLUTION OF THE PILTDOWN PROBLEM

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## INTRODUCTION

WE are now in a position to give an account of the full extent of the Piltdown hoax. The mandible has been shown by further anatomical and X-ray evidence to be almost certainly that of an immature orang-utan; that it is entirely Recent has been confirmed by a number of microchemical tests, as well as by the electron-microscope demonstration of organic (collagen) fibres ; the black coating on the canine tooth, originally assumed to be an iron encrustation, is a paint (probably Vandyke brown) ; the so-called turbinal bone is shown by its texture not to be a turbinal bone at all, but thin fragments of probably non-human limb-bone ; all the associated flint implements have been artificially iron-stained ; the bone implement was shaped by a steel knife ; the whole of the associated fauna must have been " planted," and it is concluded from radioactivity tests and fluorine analysis that some of the specimens are of foreign origin. The human skull fragments and some of the fossil animal bones are partly replaced by gypsum, the result of their treatment with iron sulphate to produce a colour matching that of the gravel. Not one of the Piltdown finds genuinely came from Piltdown. These latest investigations have demonstrated the methods now available which will not only make a successful repetition of a similar type of forgery virtually impossible in the future, but will be of further value in palaeontological research.

GAVIN DE BEER,
*Director.*

# 1. OUTLINE OF THE PILTDOWN PROBLEM

*By* J. S. WEINER

Department of Anatomy, University of Oxford

THERE are three sites on or near Piltdown Common, Sussex, to which attention was originally drawn by Charles Dawson and where in the years 1908 to 1915 fossil and archaeological remains came to light. The first site is a gravel pit alongside the main drive in the grounds of Barkham Manor, about a hundred yards from the house. Here fossils and implements were found at intervals from 1908 to 1914. Smith Woodward was first informed of the skull (here referred to as Piltdown I) in a letter from Dawson dated 14th February, 1912. The gravel itself was noticed by Dawson as a likely source of Pliocene or Early Pleistocene fossils some years earlier, possibly in 1899 (Dawson, 1913 : 75). The second site is a field (its precise situation is not recorded) probably at Sheffield Park about two miles to the north-west of the first site. Here finds (Piltdown II) were reported by Dawson in 1915. The third site is at Barcombe Mills, four miles south-west of Piltdown ; cranial fragments said to have been obtained here were in Dawson's possession at the time of his death and were obtained for the British Museum by Smith Woodward. Neither the date of this discovery nor the exact spot has been recorded. Only at Barkham Manor were any systematic excavations carried out ; these were conducted by Smith Woodward and Dawson in 1912, 1913 and 1914, by Woodward alone in 1916—the year of Dawson's death—and spasmodically afterwards (Woodward, 1948). Nothing was found in the 1916 season, nor when gravel was dug at another spot nearer the farmyard some years later. The original site was re-excavated in 1950 under the auspices of the Nature Conservancy and a new trench dug to provide a permanent witness section of the Piltdown gravel (Toombs, 1952), but nothing human or animal came to light. The material from all three sites is considered in this report.

The bibliography on Piltdown is very large ; over 300 references were listed by W. & A. Quenstedt (1936), and a select list was given by Oakley (1952). The teeth and the cranial and mandibular fragments (Piltdown I and II) were described by Woodward (Dawson & Woodward, 1913, 1914 ; Woodward, 1917), and by Keith (1925), and the Barcombe Mills skull fragments by Ashley Montagu (1951). Accounts of the animal remains have been given by Woodward (Dawson & Woodward, 1914, 1915) and by Hopwood (1935). The flint implements were dealt with by Dawson in the first publications and by Woodward in *The Earliest Englishman* (1948). The unique bone implement was the subject of a special paper (Dawson & Woodward, 1915).

The circumstances and sequence of the finds, which have an important bearing on the controversies arising from Smith Woodward's interpretation and on the final invalidation of his conclusions by the disclosure of the fraudulent nature of the material, will be dealt with by one of us (J. S. W.) in a forthcoming book to be published by the Oxford University Press.

Smith Woodward accorded the finds at Barkham Manor full recognition as a new genus and species of the Hominidae—*Eoanthropus dawsoni*—of Early Pleistocene age, " defined by its ape-like mandibular symphysis, parallel molar-premolar series, and narrow lower molars which do not decrease in size backwards ; to which diagnostic characters may probably be added the steep frontal eminence and slight development of brow-ridges". Both the dating and the attribution of the remains to one individual were challenged at the first announcement of the discovery on 18th December, 1912. Newton and Keith favoured a Pliocene date (Dawson & Woodward, 1913), but the majority agreed with Dawson's and Woodward's Lower Pleistocene estimate, which remained undisputed until Edmunds, in 1925, made a new geological survey of the East Sussex region. In 1935 Hopwood placed the skull and jaw with the derived Villafranchian remains. The anatomical conclusion was disputed strongly by Waterston from the start (in Dawson & Woodward, 1913 : 150 ; Waterston, 1913) and by Miller (1915), Boule (1915), and others. To these authors the combination of a skull and mandible of such distinct types in a single individual seemed, on morphological grounds, highly improbable. They pointed out that the skull bones, if found by themselves, would certainly have been referred to the genus *Homo*, and the mandible, if found by itself, would as certainly have been accepted as that of an anthropoid ape. Thus two distinct forms were presumed to be present —fossil *Homo sapiens*, and a fossil ape named *Pan vetus* by Miller (1915) and *Boreopithecus dawsoni* by Friederichs (1932).

None the less, the evidence and arguments put forward by Woodward made a coherent and convincing case which was enormously strengthened by the finding of the canine in 1913 and Piltdown II in 1915. Keith restated and extended this case in 1915, giving his support to Woodward's thesis after careful weighing of the evidence. Not for many years could the evidence in any respect, anatomical, geological, archaeological or phyletic be shown with certainty to be untenable, though a number of serious criticisms were brought forward. On the available evidence the strength of the case for *E. dawsoni* may be judged by listing the arguments urged in favour of Woodward's interpretation:

1. The probable natural association of cranium with jaw was attested by their close physical proximity, especially so in a gravel formation—the mandible " within a yard " of where one piece of occiput had been found by Woodward in an undisturbed patch of gravel (Dawson, 1913), the canine in gravel " *in situ* excavated within a radius of 5 yards of the spot where the mandible was found " ; the nasal bones and " turbinal " within 2 or 3 ft. of the mandible.
2. The complementary nature of the fragments—mandible, canine and jawless cranium—in such close physical proximity pointed irresistibly to their natural association.
3. The state of mineralization, colour, and unrolled condition of the different pieces appeared very similar. The canine tooth, like the bony fragments, was apparently iron-stained.
4. There was positive anatomical evidence of the natural association between

lower jaw and cranium. In particular, the remarkable flat wear on the molars was a human and not an ape-like character, and functionally in entire accord with the human type of articulation of the glenoid cavity.

5. The canine in its wear also indicated a complete departure from the normal ape-like condition. The canine could not have overlapped in the normal simian fashion with the corresponding tooth in the opposing jaw since there is no attrition facet on either the proximal or distal aspect of the tooth.

6. The X-ray appearance of the roots of the molar tooth was much more reminiscent of the human than the ape condition (Keith, 1925).

7. Other arguments, of less weight than the foregoing, were (i) Pycraft's (1917) belief that the axis of alignment of the molar teeth in the jaw was much more like man than ape, (ii) Elliot Smith's view that the endocranial cast showed simian features and (iii) Woodward's (1932) inference that the order of eruption was human and not ape-like based on the much greater attrition suffered by the canine in comparison with that of the molar.

8. As a further refutation of the idea that the association of jaw and cranium was an accidental coincidence, there was the discovery of Piltdown II. The finding of another molar of the same type as those of Piltdown I, also associated with cranial fragments denoting a second individual not distinguishable from *Homo*, increased very greatly the probability of the natural association of mandible and brain-case.

9. The combination of hominid skull with ape-like jaw was not inadmissable on grounds of morphological incompatibility since there are many fossil instances of quite unexpected combinations of skeletal structures.

10. The existence of a creature like *E. dawsoni* was consistent with its reported geological age, as judged by associated fossils and the apparently " pre-Chellean " tools, for an ancestral or transitional form of this kind was to be expected in the Lower Pleistocene.

11. " Piltdown Man " was more simian than Heidelberg Man. Though morphologically very different from *Pithecanthropus* (then known only by skull cap, two doubtful molars and a disputed femur) it had as good a claim to represent the ancestor of *H. sapiens* since in brain size it was far more advanced than *Pithecanthropus*.

Woodward's interpretation was thus a close-knit set of arguments which took all the evidence into account. The alternative hypothesis that the discoveries represented two distinct creatures—fossil man and fossil ape—could not account for all the evidence without raising new complexities. To avoid the acceptance of Piltdown II as a second remarkable coincidence some doubted its authenticity. Hrdlicka (1922) suggested that the isolated molar must have come from the first site and that some mistake had been made—a suggestion denied by Woodward (1933). Weinert (1933) thought that the frontal bone of Piltdown II really belonged to Piltdown I. Weidenreich (1937) supposed that the isolated molar was human, so making Piltdown II a discovery of prehistoric *H. sapiens* only.

An anatomical argument against the association of the cranium with the mandible is that the bicondylar width of the mandible does not correspond to the distance between the mandibular fossae on the base of the skull, and therefore it is impossible to fit the mandible to the skull. But the symphysial region of the mandibular fragment is missing, and with no certain evidence of the position of the mid-line of the mandible there can be no certainty in estimating the bicondylar width.

However much evidence of the ape-like character of the mandible was brought forward (Miller, Ramström, Friederichs), the inference that the missing crucial condylar region would also be ape-like remained incapable of proof. With so much else ape-like, a variety of suggestions were made to account for the " un-ape-like " dental wear. Miller (1915) thought that similar flat wear might occasionally occur even in modern apes. The specimen which he adduced, however, was not only unusual but quite abnormal (Pycraft, 1917). Weidenreich (1937) drew attention to flat wear in the molars of a Pleistocene orang in Mme. Selenka's collection from Java but he only reproduced a photograph of this specimen and made no detailed comparison with the Piltdown molars. Both he and Miller left the peculiar wear on the canine unexplained. Marston (1952) has attempted to go further and has theorised as to the movements which might produce the Piltdown wear, supposing that the canine were an upper canine. But that such movements were ever made by a jaw with a structure, so far as it is known, and muscular attachments indistinguishable from that of modern apes remains completely hypothetical.

Nevertheless, certain of the criticisms of Woodward's conclusions cannot be disregarded. In particular, the " human " features said to exist in the mandible and teeth are few indeed (though they are crucial), whereas detailed study serves only to emphasise the astonishing similarity of the mandible to that of a modern orang or chimpanzee. Sicher's study (1937) deserves mention here, for, impressed by the completely non-human configuration of the dental foramen and its relation to the mandibular canal, Sicher questioned the association of the jaw and cranium. Keith (1925) himself did much to throw doubt on certain alleged simian features of the braincase and endocranial cast brought forward by Elliot Smith. Symington (1915) severely criticized the latter's conclusions, and could find no convincing evidence of any precocious or peculiar development in the brain of *Eoanthropus*. Lyne (1916) drew attention to the extraordinary contradiction between the apparent immaturity of the canine and its excessive wear, but his explanation that the tooth might be a milk canine had little to support it and his important observations were disregarded. Miller (1918) and Marston (1952) threw doubt on Pycraft's belief in the " near-human " alignment of the molars in the jaw. Doubts had early been expressed on the workmanship of the bone implement (Reginald Smith, in discussion of Dawson & Woodward, 1915 ; Breuil, 1938) ; these were renewed by Oakley in 1949.

The interpretations of Woodward and his critics were beset with new difficulties when fluorine tests (Oakley & Hoskins, 1950) showed that *E. dawsoni* could not be accepted as a Late Pliocene derivative, but was apparently contemporary with the gravel. Combined with Edmunds' conclusion of 1926, this implied the dating of the remains to the last interglacial period, i.e. the early part of the Upper Pleistocene. These difficulties were further enhanced from about 1925 onwards by many new discoveries of *Pithecanthropus* (both in Java and China), of the Australopithecinae and of fossil apes (particularly in E. Africa.)

By 1950 every possible opinion of " Piltdown Man's " status had been discussed. Weidenreich (1947) had decided to dismiss the " chimaera " altogether ; Friederichs (1932), Montagu (1951), Marston (1952) and others believed that the remains represented two distinct fossil creatures ; some (Howells, 1947 ; Leakey, 1953) felt that the situation was so confused that no definite decision could be made ; others, that the matter should be left in " suspense account " (Le Gros Clark, 1949) in the hope that more material might be found ; and there were some for whom " *Eoanthropus dawsoni* " continued to figure unquestioned as a species or genus of the Hominidae. Finally, Weinert (1953) thought that the jaw, if properly reconstructed, would turn out to be hominid and by no means ape-like.

### *The hypothesis of a fake or hoax*

In the new situation created by the revised dating the only two conceivable " natural " explanations both seemed entirely inadequate on evolutionary grounds and the many puzzling anatomical features remained unresolved. How else could all the apparent facts be explained ?

The possibility had to be faced that the Piltdown finds were a hoax—that the mandible was indeed that of an ape, but of a modern ape so treated by mutilation of the fragment, abrasion of the teeth and staining as to appear a genuine fossil. Not only could this hypothesis at once explain the circumstances of the finds and the sequence of discoveries, it could also be entertained on the following grounds:

(1) That the only morphological feature in the mandible which could not be said to be ape-like was the wear on the molars and it seemed surprising that this should be the only undoubted feature to link the cranium and mandible.

(2) That filing down of chimpanzee and orang molars was found to produce an appearance similar to that of the Piltdown molars.

(3) That artificial abrasion would explain the baffling and unique wear of the canine.

(4) That the very parts of the mandible which one would expect a faker to remove were, in fact, broken off.

(5) That Oakley (in 1949) found the dentine under the thin, dark " ferruginous " layer to be "most unexpectedly—pure white". (Oakley & Hoskins, 1950 : 381).

(6) That the 1949 fluorine analysis had left the antiquity of the mandible quite indeterminate. It had, in fact, " failed to differentiate *Eoanthropus* from Holocene bones". (Oakley, 1951 : 50).

(7) That an element of doubt already surrounded the bone implement.

An exhaustive re-examination of all the Piltdown finds has completely confirmed the hypothesis of a hoax, and experimental work has shown that all the features of the Piltdown teeth and jawbone can be reproduced artificially. The main results have already been published (Weiner, Oakley & Le Gros Clark, 1953). The present series of reports gives the evidence in greater detail and covers a wider field.

# 2. AN ANATOMICAL STUDY OF THE PILTDOWN TEETH AND THE SO-CALLED TURBINAL BONE

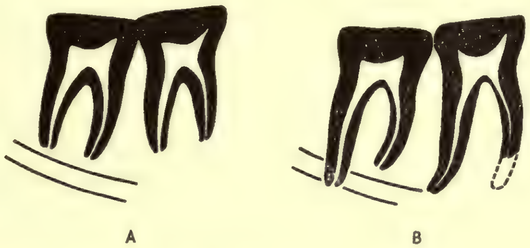
*By* W. E. Le GROS CLARK, F.R.S.

Department of Anatomy, University of Oxford

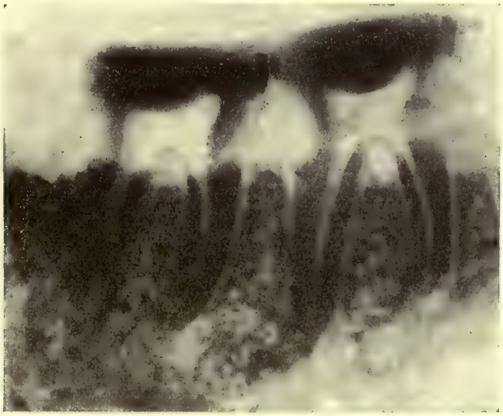
## (I) THE ANATOMICAL DETAILS OF THE PILTDOWN TEETH

The teeth from Piltdown are the first and second right lower molars in the mandibular fragment, an isolated canine tooth, and an isolated left lower molar tooth. The last was reported to have been found in a heap of stones raked off a ploughed field about two miles from the original Piltdown site. Considered by themselves, it seems certain that the teeth would have been attributed to an anthropoid ape (quite similar to a chimpanzee or an orang) except for two main features : (1) the extremely flat wear of the molar teeth in the mandible, which is not normally to be found in pongid teeth at an equivalent stage of attrition, but which closely approximates to the type of wear commonly found in hominid molars ; and (2) the quite unusual type of wear on the canine which, so far as we are aware, is not paralleled in the canines of any of the known genera of anthropoid apes, recent or extinct. The suggestion that these aberrant features might be the result of artificial abrasion at once offered a plausible explanation of their seemingly anomalous character. Indeed, it may well be asked why such a suggestion had not been seriously considered until quite recently. There are no doubt several reasons for this. In the first place, the mandibular fragment and the canine tooth were reported to have been found by experienced palaeontologists during their excavations at Piltdown, and the occurrence *in situ* has thus always been accepted without question. Secondly, the faking, obvious though it now appears, had been accomplished with extraordinary skill ; and, lastly, the statement that the worn surface of the canine shows an exposure of secondary dentine would almost certainly have distracted attention from a possible consideration of faking by artificial abrasion. Secondary dentine is deposited as a reaction to prolonged natural wear and its presence in the canine would thus presuppose that the excessive wear of this tooth was indeed natural. In fact, a re-examination of the canine has shown that there is no evidence of the deposition of secondary dentine.

Two other relevant features have been held by some authorities to distinguish the Piltdown molars of the mandible from those of anthropoid apes. One is their hypsodont character. But comparative study has shown that, while a similar degree of hypsodonty is very unusual (if, indeed, it does occur) in chimpanzees and gorillas, it is not uncommon in the orang. The other feature is the relative shortness of the roots of the molar teeth as they appeared to be displayed in the original radiograph of the Piltdown molars published in a paper by Underwood (1913) and subsequently copied in publications by other authors (e.g. Keith, 1915; Lyne, 1916). But new radiographs taken recently show quite clearly that the roots are in fact markedly longer than they have been portrayed, and are thus entirely simian in appearance. This seems to us to be an important point which needs to be emphasized. The original radiographs lacked sufficient definition to outline the roots distinctly: from the recently taken radiograph the outlines of the molars have been reproduced for comparison with those made from appearances shown in the original radiograph (Text-figs. 1, 2). It will be observed that the lower end of the anterior root of $\overline{M1}$



TEXT-FIG. 1. A. Outline drawing of the molar teeth in the Piltdown mandible showing the roots as they had been interpreted on the basis of the original radiograph published in 1913. B. A similar drawing made from a recent radiograph showing the actual form and extent of the roots. The anterior root of $\overline{M1}$ has been broken off, and its probable extent is indicated by a broken line. In both figures the position of the mandibular canal is shown. Natural size.

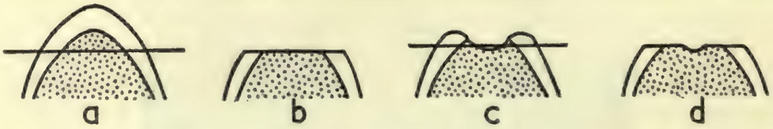


TEXT-FIG. 2. Radiograph of the two molar teeth in the Piltdown mandible showing the form and extent of their roots. Note the apparently accurate apposition of the crowns of the teeth at their contact facets. Twice natural size. [*X-ray by P. E. Purves.*]

has been broken off (presumably it has been involved in the fracture of the mandible at this level). Its total length can therefore not be precisely estimated, but there is an indication of the lower end of the socket which suggests that originally the apex of the root curved downwards and backwards for some distance. The posterior root of $M\overline{1}$ is long and is deflected backwards at its lower extremity. The radiograph of the mandible shows that it actually reaches the upper border of the mandibular canal. The anterior root of $M\overline{2}$ is well defined and was correctly displayed in the original radiograph. Compared with the posterior root of $M\overline{1}$, the rounded and blunt apex of this root and the relative width of the apical canal suggest that the root had perhaps not completed its full development. The posterior root of $M\overline{2}$ is considerably longer than the anterior root, extending downwards to the level of the lower border of the mandibular canal. This relationship is of some significance, for the " hominid " appearance in the original radiograph showing the roots of both the first and second molars apparently falling well short of the canal certainly misled some authorities. Like the anterior root, the apex of the posterior root of $M\overline{2}$ is bluntly rounded and the apical canal relatively wide.

The problem having been posed—is the unusual type of wear of the Piltdown molar teeth the result of natural attrition during life or of artificial abrasion after death ?—consideration was given to those details which on close inspection might be expected to differentiate the one from the other. A critical study of the teeth at once revealed certain features which had either escaped notice previously, or the possible significance of which had not been realized. Indeed, it was because these features appeared to lend such strong support to the hypothesis of artificial abrasion that it was decided to re-examine all the Piltdown material for further evidence of faking.

The flatness of the molar teeth is astonishingly even over almost the entire extent of the occlusal surface, as though, indeed, the latter had been planed down by some rapidly acting shearing force. A considerable area of dentine (about 4 mm. in its greatest diameter) has been exposed on the antero-internal cusps of both teeth, and not only are these areas quite flat, they are also flush with the surrounding enamel (Text-fig. 3, *a*, *b*). But in natural attrition, whether in hominids or pongids, areas



Text-fig. 3. Diagram illustrating the peculiar type of abrasion on the cusps of the Piltdown molar teeth. In (*a*) is shown a schematic section through an unworn cusp. If this were subjected to artificial abrasion in the plane indicated, the appearance shown in (*b*) would be produced, i.e. a flat area of exposed dentine (stippled) flush with the surrounding enamel; such an appearance is seen on the antero-internal cusps of the Piltdown molars. In (*c*) is shown a schematic section through a cusp partially worn by natural attrition, illustrating the concavity of the dentine depressed below the surrounding enamel. Artificial abrasion in the plane indicated would produce the appearance shown in (*d*), i.e. a depressed " dimple " in the centre of a flat area of dentine flush with the surrounding enamel ; such an appearance is seen on the antero-external cusps of the Piltdown molars.

of dentine exposed to this degree form shallow concavities, because the less hard dentine wears away more rapidly than the surrounding and harder enamel. The possibility that the appearance of the occlusal surfaces of the Piltdown molar teeth might be the result of an unusual type of natural attrition, which had proceeded so rapidly that there was insufficient time for the exposed dentine to be hollowed out below the level of the surrounding enamel, does not seem an acceptable explanation. In the first place we have not been able to find, in an examination of 137 ape jaws and 200 human jaws, a parallel condition in areas of dentine of similar extent exposed by natural attrition. Secondly, the small punctate exposures of dentine on the external cusps of the Piltdown molars are in fact already depressed below the surrounding enamel, presumably as the result of natural wear (and thus indicating that the latter was originally of the normal type). Moreover, on the antero-external cusp of both molars the punctate exposure of dentine is surrounded by a small and perfectly flat area of dentine which, it appears, must have been exposed (like the areas of dentine on the antero-internal cusps) by artificial abrasion (Text-fig. 3, *c*, *d*). These flat areas of dentine are stained a brown colour and are sharply defined by a thin outline of deeper staining. We have been able to produce outlines of somewhat similar appearance in modern teeth which have been filed down and artificially iron stained, and it seems probable that the outline of deeper staining may be due to the relatively rich amount of organic substance at the dentino-enamel junction, where there is a greater proportion of interprismatic substance to enamel-rods (Noyes, 1948), and also to the considerable degree of branching and interlacing of dentinal tubules at the surface of the dentine.

Another curious feature of the molars of the Piltdown mandible is that the dentine on both $M\overline{1}$ and $M\overline{2}$ is much more extensively exposed on the antero-internal than the antero-external cusps. But this is the reverse of natural wear, in which the outer cusps of the lower molars are normally worn down more rapidly in the earlier stages of attrition. Out of 200 human jaws there were only 4 in which (at an approximately equivalent stage of wear) the dentine of a lower molar was exposed to an approximately equal extent on the outer and inner cusps ; in one other the area of exposed dentine on the inner cusp was rather more extensive (though by no means to the degree shown in the Piltdown teeth). Thus with normal occlusion it must be at least very exceptional to find human teeth in which the wear on the antero-internal cusps is so much greater than on the antero-external cusps of $M\overline{1}$ and $M\overline{2}$ as to be comparable with the Piltdown molars. In ape molars also, so far as we have been able to determine from the evidence of 137 jaws of the modern large anthropoid apes, as well as 38 specimens representing 9 different genera of fossil apes, the wear is normally greater on the outer cusps. In no case did we find a lower molar tooth showing the reversed condition seen in the Piltdown molars (though in one female gorilla there were small punctate exposures of approximately equal extent on the antero-internal and antero-external cusps of $M\overline{1}$). This evidence makes it difficult to explain the relative wear of the outer and inner cusps of the Piltdown teeth except by the hypothesis of artificial abrasion.

This inference is further supported by the sharp edges with no bevelling which bound the flat occlusal surfaces of the molars at their margins. The absence of bevelling at the external margin seems particularly significant, for normally this margin shows distinct bevelling caused by the overlap in occlusion of the external cusps of the upper molars. In only 10 out of 200 human jaws was the lateral margin of the lower molar teeth found to be as sharp-cut as those of the Piltdown mandible (but these exceptions did not show the other unusual features of the supposedly fossil specimens). The sharpness of the edge in the Piltdown molars is consistent with the postulate of artificial abrasion, and a similar appearance is to be seen on the talonid basin of the second molar. This depression, which is still relatively unworn, is also separated from the quite plane occlusal surface of the crown by a sharp unbevelled edge. We have not been able to find a similar feature in our series of ape and human jaws in which the lower molars have been exposed to natural attrition. For, in normal occlusion, the protocone of the upper molar fits into the talonid basin of the opposing lower molar and in normal wear produces a sloping rounded edge at the margin of the depression. On the other hand, the sharp unbevelled edge seen in the Piltdown molar would be expected to result from an attempt to produce a flattened surface by artificially planing down a more or less unworn tooth. Examination of the occlusal surfaces of the two molars under a binocular microscope provides further evidence, for here and there the enamel and dentine are scored with extremely fine scratches, sometimes disposed in a criss-cross pattern. Such scratches, which are not apparent to the same degree over the enamel on the sides of the crowns, strongly suggest the application of an abrasive of some sort.

A further point to notice in the first and second molars of the Piltdown jaw is that they both show almost exactly the same degree of wear. But normally the wear of the first molar is distinctly more marked, since it has been longer in use. Exceptional cases, however, do occur in human lower molars in which the wear of the two teeth is approximately equal, and it may happen that the second molar is the more severely worn as the result of some defect in the upper dentition. In our series of 137 ape jaws, we have only found three instances (chimpanzees) in which the first and second molar teeth are worn to about the same degree. It appears, therefore, that the condition in the Piltdown molars is at least very unusual.

One more suggestive feature is to be seen in the mandibular molars—their occlusal planes are not quite congruous, i.e. they do not fit together to form a uniform contour. The posterior margin of $M\overline{1}$ at its inner end projects about 2 mm. above the adjacent anterior margin of $M\overline{2}$, and the occlusal plane of $M\overline{1}$ is set at a slight angle to that of $M\overline{2}$. On the other hand, the outer end of the posterior margin of $M\overline{1}$ is level with the adjacent anterior margin of $M\overline{2}$. The possibility that this might be due to a post-mortem displacement of $M\overline{1}$, the occlusal surface of the latter having as a result been rotated slightly outwards about the axis of its outer margin, is negatived by two observations: (1) the radiograph of the molar teeth in lateral view shows that their roots fit accurately into their sockets, and (2) there is no sign of a contact facet on the exposed posterior surface of $M\overline{1}$ (which might be expected if this tooth had been displaced upwards relative to $M\overline{2}$). Radiographs of the teeth in lateral view also appear to show the contact facets between them in accurate apposition (see Text-fig. 2). It is true that the two molars are not in exact symmetrical alignment, but this is a common feature in an immature mandible in which the eruption of the permanent dentition is in process of final completion and in which the second molar has not completely rotated to its final position in the alveolar border. On the other hand, a recent radiograph of the teeth from their occlusal aspect shows a slight gap between the anterior root of M$\overline{1}$ and the inner wall of the socket, suggesting a slight displacement outwards of the tooth. Even so, it still would not be possible with the slight readjustment which would be necessary to correct it, to bring the occlusal planes of the two molars into precise conformity, the more so because the posterior margin of M$\overline{1}$ is slightly concave in contrast to the quite straight anterior margin of M$\overline{2}$. This evidence of the lack of conformity between the occlusal plane of the two teeth adds further support to the hypothesis of artificial abrasion, for it suggests that the process of paring down has been applied separately to each tooth. Taken by itself, this is not perhaps entirely conclusive, for as the result of mal-occlusion resulting from some defect of the upper dentition incongruities may occasionally occur in teeth exposed to natural attrition.

The enamel bordering the dentine exposure on the antero-internal cusps of M$\overline{1}$ and M$\overline{2}$ has been cracked and chipped, and on M$\overline{2}$ a small flake has evidently become detached and been replaced in position with some adhesive. We have found in our experimental grinding of molar teeth that this type of cracking and chipping of the enamel is very liable to occur, though it can be minimized by embedding the teeth in plaster of Paris, and it is therefore of particular interest to find that the Piltdown molars are similarly affected.

The radiograph demonstrates the presence of a small lobulated odontoma in the pulp cavity of M$\overline{1}$, an unusual feature which, however, has no particular relevance to the Piltdown problem.

The isolated lower left molar (probably M$\overline{1}$) reported to have been found in a heap of stones raked off a field two miles from the site of the Piltdown excavations is so closely similar in dimensions and shape to the mandibular molars that it probably belonged originally to the same individual. However, it does not show the same degree of flat wear and, no doubt for this reason, some authorities have refused to associate it with the Piltdown jaw. But if the wear of the molars has been artificially produced, such an objection no longer remains valid. An examination of this isolated tooth with a binocular microscope shows that the enamel on the occlusal surface of the crown is scored with fine scratches, similar to, but rather coarser than, those already noted on the mandibular molars.

The evidence of the isolated canine tooth found in 1913 is consonant with that of the molars. The radiological evidence that this tooth had not yet completed its full development appears to be sound. The pulp cavity is widely open at the apex of the root, and even if this is assumed to be the result of post-mortem damage, it would not account for the relatively large size of the cavity as a whole. But, if the tooth is immature, it is difficult to explain the severe degree of attrition of the lingual surface of the crown unless it has been artificially produced.[1] For the entire thickness of the enamel has been removed over the entire extent of the lingual surface, from the anterior to the posterior border of the crown. Over a small area just above the middle of the worn surface the dentinal wall of the pulp cavity has been reduced to a thickness of less than 1 mm., and at one point the pulp cavity has actually been penetrated. At that point a rather curious feature is seen in the radiograph, for it appears that the opening into the pulp cavity has been plugged with some plastic material which is not itself radio-opaque (but which contains some fine dust-like particles which are radio-opaque).[1] Further, the radiographs show no evidence of the deposition of secondary dentine, with a narrowing of the pulp cavity, such as might be expected if the severe attrition of its lingual surface had been naturally produced. It is now clear that, in the original descriptions of the tooth, the material used for plugging the opening into the pulp cavity was mistaken for secondary dentine. Apart from the severity of the wear of the canine, the pattern of attrition is quite unlike that found in any ape (recent or extinct), whether the canine belongs to the upper or lower dentition. It has, indeed, been argued that such a type of wear might be theoretically possible in an ape's jaw, given certain unusual occlusal relationships and movements of the jaw, but (apart from the questionable validity of these arguments) the fact is that it has never been demonstrated to occur in any known pongid or hominid. The contour of the worn surface is in fact peculiar, for while it is evenly concave in a vertical direction it is almost flat from before backwards and it is not accompanied by an attrition facet on the anterior or posterior margin of the tooth.[2] It is exceedingly difficult to imagine an occlusal relationship which could have produced such a contour by natural wear, and it is little wonder that in the early discussions on the Piltdown " fossil " there was some controversy whether the attrition was caused by contact with the opposing canine or lateral incisor tooth. On the other hand, the contour of the worn surface is quite consistent with the surmise that the latter was abraded by artificial means.

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[1] The large size of the pulp cavity had been noticed many years ago by Lyne (1916), but he sought to explain the combination of this feature with the severe wear on the assumption that the tooth is a deciduous canine of unusual size.

It may be argued that at least some of the details of the Piltdown teeth which have been described, when considered separately, are inadequate by themselves to confirm the thesis that the teeth have been deliberately fabricated to simulate fossil specimens. But when they are taken together we are forced to the conclusion that they could not possibly have been produced other than artificially.

In attempting to decide whether the jaw and teeth are those of an orang or a chimpanzee, one must remember that the artificial abrasion has removed or otherwise damaged the finer details of dental morphology which distinguish these two genera. Even so, it is possible to say that they are almost certainly those of an orang. Thus, the hypsodont character of the molars and the size and shape of their pulp cavities are quite similar to those of orang teeth (Text-fig. 4), but differ markedly from those of chimpanzees which we have examined. Again, the pattern of the dentine exposure corresponds very closely to that produced in our experimental abrasion of orang molars, and the numerous small fissures and pits in the central part of the occlusal surface are clearly the residual traces of crenulations of some complexity. Indeed, in one orang jaw in which we abraded the first and second molar teeth, they were found to duplicate the appearance of the Piltdown molars to a remarkable degree, not only in the extent and the contour patterns of the dentine exposures on the several cusps, in the size, depth and abrupt margins of the central basin, and in showing an approximately similar residuum of crenulations, but also in the general proportions of the crowns as a whole (including their height as measured above the enamel margin). See Pl. 27.

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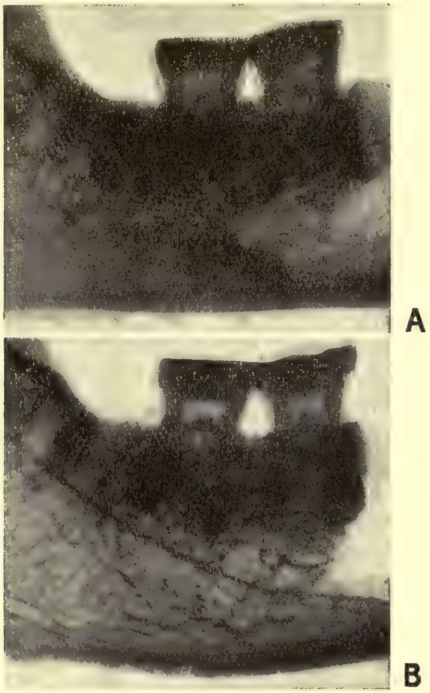
[1] The penetration of the pulp cavity was not evident in the radiographs of the canine reproduced in the original communication of Dawson & Woodward (1914), for the reason that they did not happen to have been taken in just the appropriate plane.

[2] When the canine tooth was picked out of a heap of gravel in 1913, it was found accurately to resemble in shape the plaster model of the canine which had already been reconstructed to fit the Piltdown mandible. Commenting on the discovery in a postscript dated 16th September, 1913, Underwood (1913) wrote " The tooth is absolutely as modelled at the British Museum."



TEXT-FIG. 4. Radiographs of (A) the Piltdown molar teeth, compared with (B) those of the female orang mandible shown in Pl. 27, fig. 2. The orang is evidently more fully mature than the fossil specimen, as shown by the slightly smaller size of the pulp cavities and narrower root canals of the molars, and by the fact that the mandible as a whole is a little more robust. (For a radiograph of orang molars showing pulp cavities of practically identical size and shape with those of the Piltdown teeth, see Weidenreich, 1937, fig. 320). [*X-rays by P. E. Purves* (A) and *G. M. Ardran* (B).]

### (II) THE " TURBINAL BONE "

In the supplementary note on the discoveries at Piltdown (Dawson & Woodward, 1914), Dawson stated " I saw two human nasal bones lying together with the remains of a turbinated bone beneath them *in situ*. The turbinal, however, was in such bad condition that it fell apart on being touched, and had to be recovered in fragments by the sieve; but it has been pieced together satisfactorily". The only other reference to this find was made by Woodward in the same communication, and is limited to the following statement: "The remains of a turbinal found beneath the nasal bones are too much crushed and too fragmentary for description; but it may be noted that the spongy bone is unusually thick, and has split longitudinally into a series of long and narrow strips." No reason was given for identifying the fragments as those of a turbinal (it is clear that a maxillo-turbinal bone is meant to be indicated by this term), except presumably by implication its proximity "*in situ*" to the nasal bones. Moreover, contrary to Dawson's statement, the tiny fragments (eight in number) are separate and it is not possible to fit them together to form a complete bony element.

From an examination of these fragments it is clear that, whatever their true identification may be, they are certainly not those of a turbinal bone. They show none of the characteristic features of the maxillo-turbinal (such as its extreme thinness or its pitted and cellular texture). On the contrary, the fragments are relatively thick and they show a longitudinally grained texture which indicates that they are composed of Haversian systems arranged in parallel formation. Presumably, therefore, they are derived from the shaft of a limb bone (probably of some small animal), but their precise identification is indeterminate.

# 3. THE PILTDOWN "IMPLEMENTS"

*By* K. P. OAKLEY

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### (I) THE FLINT "IMPLEMENTS"

DAWSON recorded that the Piltdown gravel is composed of Wealden ironstone pebbles, mixed to the extent of about one-sixth of the mass with angular brown flints, a large proportion of which are tabular in form with fractured edges, frequently conforming to the so-called eoliths of the Plateau Gravels. He was duly cautious with regard to eoliths. "Whether natural or artificial, the fractures appear to have been largely governed by the prismatic structure of the flint" (later he introduced the term starch-fracture to describe breakage of this type). He pointed out that the rolled examples had a deep iron-stained patina, whereas the unrolled ones were less deeply stained and patinated. He said that there also occurred in the Piltdown gravel "certain brilliantly coloured iron-red flints, presumably more highly oxidised than the prevailing flints, which were of a brown colour." He continued: "Among the flints we found several undoubted flint-implements, their workmanship being similar to that of the Chellean or pre-Chellean stage; but in the majority . . . the work appears chiefly on one face of the implements."

Only four of these "Palaeolithic implements" were figured by Woodward and Dawson in their joint papers, as follows:

*E*.605. (Pl. 28, fig. 3B). Side-blow flake of pointed foliate form, 9 cm. × 5 cm., with maximum thickness 2·5 cm.

The whole surface is patinated and stained yellowish-brown, the edges are dulled. See Dawson & Woodward 1913, pl. XVI, 1, *1a, b*; Sollas 1924, fig. 81; Woodward 1948: 40, fig. *9a*.

According to some unpublished notes, Woodward found this "best formed tool" loose in one of the heaps of gravel rubbish at the main site.

*E*.606. (Pl. 28, fig. 3C). Triangular bifaced point, with area of smooth brownish stained cortex at the butt; 8 cm × 6 cm., with maximum thickness of 2·5 cm. The flaked surfaces are patinated with a superficial pale yellowish brown stain, the edges are dulled. See Dawson & Woodward, 1913, pl. XVI, 2, *2a*; Woodward 1948: 40, fig. 8*a*.

This "palaeolithic tool" is recorded by Dawson (in Dawson & Woodward 1913: 122, footnote 1) as having been found *in situ* by Father Teilhard de Chardin, in the loamy stratum of the Piltdown gravel (see p. 275).

*E*.607. (Pl. 28, fig. 3A). Massive flake of squarish form, 14 cm. × 13 cm., with maximum thickness of 5 cm. The flaked surfaces are patinated and stained bright orange, the edges are dulled. See Dawson & Woodward, 1913, pl. XVI, 3, 3*a*, *b*; Breuil, 1949, fig. 4. According to unpublished notes by Woodward this specimen was found by Dawson on a heap of gravel rubbish at the main site.

*E*.613. Heavily rolled, oval end-struck flake, 6·5 cm. × 5 cm., 1·5 cm. thick, of dark greyish flint with thin buff patina, the surface of which has a patchy, dark red ferruginous stain. See Dawson & Woodward, 1914: 84, pl. XIV, 1*a–c*; Breuil, 1949: 344, fig. 1; Oakley 1949, fig. 30.

This is the only artifact which was recorded as having been found *in situ* in the dark brown basal gravel.

The first three specimens have a number of features in common:

(1) Although for the most part fractured by human agency, the form of each appears rather more accidental than intentional; (2) each is an atypical artifact, not referable with certainty to any particular culture; (3) each is in flint of a quality not found as unworked pieces in the Piltdown gravel; (4) the patina of each artifact has a ferruginous staining which is unusual in its bright colour (varying from orange to light yellowish brown) and in its patchy, rather stippled appearance (Pl. 28, fig. 4); (5) each specimen shows evidence of some heavy localised battering (Pl. 28, fig. 3 A–C) on the original exterior or cortex of the flint prior to its being flaked from the parent block.

The peculiar staining and the lithology of these three specimens are exactly matched by a core which was discovered recently in a cabinet formerly belonging to the late Mr. Harry Morris of Lewes. This specimen (Pl. 28, fig. 3D) is now preserved in the British Museum (Natural History). In an accompanying note, Morris drew attention to its similarity to the worked flints from Piltdown, and claimed that to his own knowledge this flint had been artificially stained. The patina itself appears to be natural, so the flaking is prehistoric, but judging from the style of work it is probably Mesolithic or Neolithic rather than Palaeolithic.

When dilute hydrochloric acid is applied to the surfaces of the Piltdown "palaeoliths" and Morris's flint the orange or yellowish brown stain is dissolved and can be wiped off, leaving a pale yellowish or greyish white surface of patina. In marked contrast, it has been found that the brown patina of the "eoliths" and of other flints collected from the Piltdown gravel, is unaffected by hydrochloric acid. (Pl. 28, figs. 5, 6).

Experiments carried out in collaboration with Dr. A. A. Moss in the laboratory of the Mineral Department of the British Museum have shown that the colour of the orange and yellowish or reddish-brown stained flints from Piltdown can be reproduced by dipping white-patinated flints in a solution of ferric chloride of various strengths and then treating the wet stain in ammonia fumes to produce ferric oxide.

The surface stains of a number of flints from Piltdown, including the figured ones, were first tested for us by Dr. E. T. Hall in the Clarendon Laboratory, Oxford, using his X-ray spectrographic method of analysis (Hall, 1953). The stains proved to be entirely ferruginous, with the notable exception of the yellowish-brown stain on E. 606 which contained in addition to iron appreciable traces of chromium (Table I). This result was confirmed by Dr. A. A. Moss, using a direct chemical method of analysis. Since chromium was not detected in the Piltdown gravel, or in any other flints from the gravel, there can be no reasonable doubt that this implement has been artificially stained.

TABLE I.—*Composition of stains on Piltdown flints*

| Specimen | | Estimations by E. T. Hall (in milligrams per sq. cm.) Fe | Cr |
|---|---|---|---|
| E.605 | " Palaeolithic tool " | 0·8 | nil |
| E.606 | " Palaeolithic tool (*in situ*) " | 0·5 | 0·2* |
| E.607 | " Palaeolithic tool " | 1·4 | nil |
| E.613 | " Palaeolithic flake " | 1·6 | ,, |
| E.685 | Flint from surface | 1·2 | ,, |
| E.956 | " Eolith " | 0·8 | ,, |
| E.965 | " Eolith " | 0·5 | ,, |
| E.985 | " Eolith " | 0·8 | ,, |
| E.989 | Palaeolithic flake-blade | 0·2 | ,, |
| E.2690 | Morris flint | 0·1 | ,, |
| Unreg. | Sample of gravel | 0·9 | ,, |

* Chemical estimation gave *circa* 0·1 mg./sq. cm.

When a small chip was removed from the stained cortex of E. 606 for chemical analysis, the staining was found to be superficial; below its surface the cortex proved to be pure white (Pl. 28, fig. 3C). Yet in brown flints normally found in the Piltdown gravel the cortex is iron-stained throughout its thickness. Flint nodules with white cortex do not occur naturally in the Piltdown district.

Apart from their orange or brownish staining the Piltdown " palaeoliths " could quite easily be matched in the flint waste found at flint-mining or chipping sites of Neolithic or later age on the Chalk Downs of Sussex. Dawson was perhaps not far from the truth when he wrote of the Piltdown " palaeoliths " as follows : " They resemble certain rude inplements occasionally found on the surface of the Chalk Downs near Lewes, which are not iron stained " (Dawson & Woodward, 1913 : 122, footnote 2). The battered aspects of these specimens (Pl. 28, fig. 3A–C), suggest that they may have originated through fortuitous shattering of flint hammerstones or anvils. Such accidentally fractured pieces are not uncommon on downland flint workshop sites. Specimens E.605 and E.606 show no signs of use, which is in accord with their being waste pieces. Some attempt has been made to shape two of the edges of the thick flake E.607, but randomly broken pieces were sometimes selected for use either as cores or as occasional tools by the Neolithic and Early Bronze Age flint workers.

Thus it appears that the only flints found at Piltdown which Dawson and Woodward considered worthy of figuring as probable palaeolithic implements show features which are difficult to explain unless they were brought to the site from elsewhere and, having been suitably stained, planted in the gravel for the excavators to find. The fact that the pieces in question are crude and atypical (in the words of Ray Lankester[1] " unlike any known or defined industry ") suggests that they may have been chosen so that they could be compared with the poorly defined and altogether dubious artifacts which had then recently been found below the Red Crag of Suffolk (Moir, 1911). Whether in fact any artifacts occur *in* the Piltdown gravel is now doubtful. No humanly fractured flint was noted during recent excavations (Toombs, 1952) ; all the artifacts previously reported were either surface finds or were introduced fraudulently.

A broken nodule of black flint with heavily bruised edges was found by Woodward in the sandy layer overlying the basal gravel ; he suggested that it may have been used as a hammerstone (Woodward 1917 : 2). In fact it bears more resemblance to a broken paving cobble bruised by cart-wheels than to a prehistoric hammerstone.

### (II) THE BONE " IMPLEMENT "

(Pl. 29, figs. 7–10)

Next to the skull, mandible and canine tooth, the most remarkable find at Piltdown (but not *in situ*) was an object shaped like the blade of a cricket bat, which had been made out of a strip of bone from the femur of a large extinct elephant. Woodward regarded it as possibly belonging to the Lower Pleistocene *Elephas meridionalis*, but it could equally well have come from one of the larger Middle Pleistocene species. Dawson & Woodward (1915) regarded the object as an implement which had been shaped by " a primitive tool, presumably a flint " when the bone " was in a comparatively fresh state." These conclusions were challenged at once when their paper was read before the Geological Society. Reginald Smith said " the possibility of the bone having been found and whittled in recent times must be considered," and A. S. Kennard doubted whether the bone had been cut when it was fresh. No comparable bone work has ever been found in known Palaeolithic industries and recent experiments have shown (*a*) that the facets on the Piltdown specimen bear no resemblance to the scratchy marks made on bone by a flint knife, nor, as Breuil once suggested (1938), to the cuts of beavers' teeth, but must have been made by an even-edged metal blade ; (*b*) that it is practically impossible to whittle a fresh or recently dried bone, which can only be worked by flaking, scraping, sawing or grinding ; and (*c*) that some fossilised bones, having more the texture of chalk, are readily carved. Plate 29, fig. 10, illustrates a fossil bone from the Swanscombe gravels which was whittled with a steel razor and then stained with a ferric solution and varnished to reproduce as nearly as possible the present appearance of the cut surfaces of the Piltdown specimen.

In conclusion, the Piltdown bone " implement " is a piece of the femur of a fossil elephant, obtained probably in two weathered pieces from a Middle Pleistocene brickearth or sandy formation. The ends were whittled with a steel knife, and the newly cut surfaces were stained with an iron solution. The small fragments of bone, now chemically shown to be from the same original source, which were found in the basal clay suggested to the excavators that the implement belonged to that level (see p. 253).

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[1] *In lit.* to A. S. Woodward, 31st Jan., 1913.

# 4. THE PILTDOWN MAMMALIA

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BETWEEN 1911 and 1914 eighteen fossil mammalian bones and teeth were found at, or in the immediate vicinity of, the Piltdown skull site. Four were recorded as having been found *in situ* in or below the chocolate-coloured basal gravel, two on the surface of the adjoining field and the remainder on the spoil heaps at the edge of the small pit. Considering the thinness of the gravel (average thickness 18 in.), the small size of the pit (less than 50 × 10 yards in area), and the extreme rarity of fossils in the Pleistocene river gravels of Sussex, this was a remarkable yield.

The fossils are heterogeneous in character, ranging from a heavily rolled enamel cap of a Mastodon tooth to a large piece of cervid antler with almost undamaged surface. Apparently they were not scattered through the gravel but were confined to one or possibly two pockets. Woodward (1948) wrote :

" After Mr. Dawson's death in 1916, I was able to open a series of pits along the other side of the hedge in a field adjacent to the original pit. There I was helped by Professor Elliot Smith ... and others. We began close to the spot where the skull was found and worked in both directions from that place. Our efforts however were all in vain. We found nothing of interest in the gravel."

In 1950 a further trench, 4 ft. × 32 ft., was dug in undisturbed gravel by the Nature Conservancy, and all the excavated material was sieved and carefully examined, but no bones nor teeth were found (Toombs, 1952).

Some of the Piltdown fossils (" *Stegodon*", *Mastodon arvernensis* and *Rhinoceros* cf. *etruscus*) are undoubtedly Villafranchian (" Upper Pliocene " of earlier authors, but now classed as Lower Pleistocene) ; but others are not older than Middle or Upper Pleistocene. When they were first described there was some question as to whether gravels of two ages were present. Dawson concluded : " It is clear that this stratified gravel at Piltdown is of Pleistocene age, but that it contains in its lower stratum, animal remains derived from some destroyed Pliocene deposit probably situated not far away, and consisting of worn and broken fragments" (Dawson & Woodward, 1913 : 123). In a later paper he wrote : " We cannot resist the conclusion that the third or dark bed is in the main composed of Pliocene drift ... " (Dawson & Woodward, 1914 : 85).

### (i) " *Derived* " *or Villafranchian Group*

With the increase of knowledge, the presence of " Pliocene " (Villafranchian) mammalian remains at Piltdown became increasingly difficult to explain, for, with one significant exception (see Table II footnote), none has been found elsewhere in southern England. If they were to be found *in situ* in Sussex, they would be expected in terrace or plateau deposits not less than 200 ft. above the level of the Ouse, but Edmunds (1926 : 68) demonstrated that the Piltdown gravel is part of a terrace 50 ft. above the Ouse (see p. 273). Thus it seemed that they could only have come from a block of indurated fossiliferous sand which worked its way down from a higher level and disintegrated on the Ouse flood-plain in 50-ft. terrace times.

When it had been established that the Piltdown mandible was a forgery it became probable that the Villafranchian fossils were also introduced in order to suggest that " Piltdown Man " dated from Pliocene times.

In his original description of one (E.596) of the three pieces of molar tooth referred to " *Stegodon* " Woodward wrote : " It cannot be referred to the upper Pliocene *Elephas meridionalis*, because in this species the valleys are deeper in proportion to their width, while the ridges are more plate-like and parallel in their upper portion. The new specimen is, therefore, of an earlier Pliocene type which is best known from the Siwalik Formation in India and has not hitherto been found in Western Europe " (Dawson & Woodward, 1913 : 142). Later, the Piltdown specimens were compared to *Elephas planiforns*, of the Upper Siwaliks, now regarded as Lower Villafranchian. There are no specimens comparable with *E. planifrons* from the English Red Crag in the British Museum nor in the Geological Survey collections. That three pieces of *Elephas* cf. *planifrons* should be recorded at Piltdown might therefore be regarded as very remarkable. In their reddish colour the Piltdown pieces resemble Red Crag fossils, and also closely match the Piltdown hominoid remains. This similarity in colour led some investigators to conclude that in spite of their unrolled condition the Piltdown skull and mandible were of Villafranchian age (Hopwood, 1935).

If the " *planifrons* " molar fragments were introduced at Piltdown it is probable that they were obtained from some foreign source and artificially stained to match the Piltdown cranial bones and mandible. The Piltdown mandible was given a rich mahogany colour by a process which involved the use of iron and chromium compounds, and it appeared likely that the same method would have been applied to imported "*planifrons*" teeth. Samples of the iron-stained cementum of the two critical specimens from Piltdown (E.596 and E.620) were analysed spectrographically in the Department of the Government Chemist by Mr. H. L. Bolton, who reported that they contain significant traces of chromium (*circa* 0·3 and 0·1% respectively).

Any remaining doubt that these pieces of "*planifrons*" molars were of foreign origin was dispelled by their radioactivity. In the hope of tracing the origin of these pieces a series of mammalian teeth from the main Villafranchian localities was included among the fossils selected for the tests (p. 276). The results obtained reinforce the conclusion that the Piltdown specimens were not obtained from an English deposit. The uranium content of fossil teeth, while increasing with geological age, is subject (as fluorine is) to considerable fluctuation from place to place. Nevertheless it appears that within relatively uniform strata of limited extent the ratio of the extremes of the variation in comparable material does not generally exceed the value of three. Thus a specimen consisting largely of dentine or cementum with a radioactivity of 200 net counts per minute is extremely unlikely to have come from a deposit such as the Red Crag in which random samples of teeth show a maximum radioactivity of less than 30 c.p.m. Uranium (again like fluorine) is adsorbed more readily by cementum and exposed dentine than by enamel, and on an average, the radioactivity of enamel in a fossil tooth is only about one-third that of dentine or cementum (Pl. 30, fig. 13). The radioactivity figures in Table II are maxima based on samples which were mainly cementum and dentine.

TABLE II.—*Radioactivity of Piltdown elephant teeth compared with mammal teeth from Villafranchian sites*

| Source of specimen | c.p.m. (Max.) |
|---|---|
| " Piltdown " (E.620) | 355 |
| " Piltdown " (E.596) | 203 |
| " Piltdown " (E.597) | 175 |
| *" Portslade " (M.10436) | 28 |
| Red Crag, Suffolk | 15 |
| Red Crag, Suffolk | 13 |
| Red Crag, Suffolk | 12 |
| Red Crag, Suffolk | 12 |
| Red Crag, Suffolk | 9 |
| Red Crag, Suffolk | 6 |
| Doveholes, Derbyshire | 25 |
| Netherlands (dredged specimen, ? leached) | 1 |
| Senèze | 15 |
| Puy-de-Dome | <10 |
| Chagny-Bellecroix | 5 |
| Val d'Arno | 26 |
| Siwaliks | 19 |
| Siwaliks | 8 |
| Algeria | 18 |
| Algeria | 15 |
| Morocco | <10 |
| Ichkeul, Tunisia | 195 |

* About 1911 the late Dr. Eliot Curwen obtained some fossils from workmen digging brickearth at Portslade, near Brighton, Sussex, including a well-preserved, grey to buff-coloured, molar of *Ursus arvernensis* (a Villafranchian species of bear) and two complete pale buff-coloured limb-bones of an undetermined species of the same genus, which he presented to the British Museum (Nat. Hist.) where they are registered under M.10436 and M.10571–2. See White 1926, pp. 85–6. The radioactivity of these three specimens proved to be higher than any of the British Pleistocene fossils which have been tested (the Piltdown specimens exluded). Their Lower Pleistocene age therefore seems assured, and since they are not in the condition of derived specimens they can have no natural place in the low-level Portslade brickearth which is Upper Pleistocene. In striking contrast a mammoth molar from the same site and undoubtedly contemporary with the brickearth proved to have a very low radioactivity. There is a strong suggestion that the specimens of *Ursus* had either been " planted " or had been traded by workmen who happened to have access to some collection of foreign fossils.

Fossils from nearly a dozen Villafranchian localities in Europe and Asia were tested, but none showed radioactivity in excess of 28 c.p.m. Professor C. Arambourg enabled us to extend the range of comparison by generously providing specimens from North African localities. A molar tooth originally recorded as *Elephas* cf. *planifrons*, from Garaet Ichkeul in Tunisia, has proved to have a radioactivity closely comparable with the Piltdown specimens. Not only is the count rate in the Ichkeul specimen and E.596 from Piltdown almost identical, but the difference between the activity of the enamel and of the cementum is unusually small in both. There is also close agreement in the fluorine content of these specimens. Ichkeul, 20 km. south west of Bizerta, is a richly fossiliferous locality, at which *Elephas* cf. *planifrons* is stated to be the commonest species represented (Arambourg & Arnould, 1950 : 155).

| | | $\frac{\%F}{\%P_2O_5} \times 100$ | p.p.m. $eU_3O_8$ |
|---|---|---|---|
| Piltdown " *planifrons* " molar E.596 | dentine and cementum | 8·2 | 610 |
| | enamel | 1·8 | 520 |
| Piltdown " *planifrons* " molar E.620 | dentine and cementum | 7·9 | 1060 |
| | enamel | 2·6 | 170 |
| Ichkeul " *planifrons* " molar | dentine and cementum | 8·4 | 580 |
| | enamel | 2·7 | <480 |
| Siwalik *planifrons* molar | dentine and cementum | 7·1 | >56 |
| | enamel | 2·0 | 45 |
| Siwalik *planifrons* molar, dentine and cementum | | 7·3 | >24 |

Proof that three Villafranchian mammalian teeth were introduced into the Piltdown gravel suggests that the others were also introduced. The molars of *Mastodon* and *Rhinoceros* showed no evidence of artificial staining, but to judge from their colour, mineralization and radioactivity, it appears probable that they were obtained originally from the Red Crag of East Anglia.

### (ii) " *Contemporary* " *Group*

Division of the Piltdown mammalia into a derived Villafranchian group and a later group contemporary with the deposition or re-arrangement of the gravel was mainly based on the known ranges of the genera and species represented ; colour and state of mineralization of the specimens were also taken into consideration. None of these criteria proved altogether satisfactory. Hopwood (1935) divided the specimens into a dark-coloured, heavily mineralized group, comprising the teeth of " *Stegodon* " (*Elephas* cf. *planifrons*), *Mastodon*, *Rhinoceros* and *Hippopotamus*, and a paler, less mineralized group, including the remains of *Equus*, *Cervus* and *Castor*. He pointed out, however, that *Hippopotamus* had never been recorded in England from deposits earlier than the Cromer Forest Bed and that the broken edges of the molar from Piltdown were sharp, suggesting that it was not a derived specimen. Moreover, the edges of two of the fragments of " *planifrons* " molars were also sharp, and since there could be no question of the geological age of these pieces, it had to be admitted that some Villafranchian specimens had found their way into the Piltdown gravel without being rolled. This important observation suggested that the dark-coloured but unrolled pieces of the Piltdown skull could belong to the older or Villafranchian fauna. This had been the opinion of E. T. Newton, and was admitted as a possibility by Dawson (in Dawson & Woodward, 1913 : 151), although he was more inclined to regard " *Eoanthropus* " as contemporary with the later, Pleistocene fauna.

The fluorine-dating method seemed a suitable means of checking the relative ages of the Piltdown remains, and the results (Oakley & Hoskins, 1950) did agree broadly with the palaeontological dating of the mammalian remains. All the undoubted Villafranchian teeth (*Elephas* cf. *planifrons*, *Mastodon*, and *Rhinoceros* cf. *etruscus*) showed a very high fluorine content (1·9–3·1%), whereas the remainder, all of which could be post-Villafranchian, showed considerably less (0·1 to 1·5%). But the range of fluorine content in the probably post-Villafranchian specimens was far greater than was to be expected in fossils of a single age-group, and it was therefore inferred that the Piltdown gravel had been re-arranged, and new mammalian remains introduced, on several occasions.

According to the results obtained, all the " *Eoanthropus* " material contained on an average the same small amount of fluorine as the bones and teeth of *Castor*. This seemed to confirm Dawson's opinion that the beaver remains were the only fossils from the pit that were contemporary with " Piltdown Man " (Dawson & Woodward, 1914 : 86).

One other fossil recorded from the Piltdown gravel showed an equally low fluorine content : the molar tooth of *Hippopotamus*, which Hopwood placed in the Villafranchian group on account of its dark colour. Its enamel is colourless and almost unaltered, but its dentine, containing $<$ 0·05% fluorine, is stained brownish black throughout. The low fluorine content appeared to indicate that it was not derived from an older geological formation, but belonged to the latest faunal group in the gravel. Yet its preservation is quite unlike that of the associated teeth of *Castor*. Considering that the "*planifrons*" molars from Piltdown had been artificially stained and then introduced at the site, the colour of the *Hippopotamus* molar suggested that it, too, had a similar history. This was confirmed by spectrographic analysis carried out in the Department of the Government Chemist by Mr. H. J. Dothie, who found that the dark-coloured dentine contained 1% of chromium, a clear indication of artificial staining.

Drs. Weiler and Strauss (see below, also Table V) showed that this tooth has an unusually high ash content, and a correspondingly low organic content. This and its exceptionally low fluorine content suggests that it could only have come from a limestone cave deposit, in which fluorination of bones and teeth is usually minimal, *Hippopotamus* has only somewhat rarely been reported from British caves, but occurs abundantly in the calcareous cave deposits of the Mediterranean islands. Some of the molars from the Ghar Dalam Cave in Malta correspond in size with the Piltdown specimen, and have a low fluorine content combined with a low organic content. The Maltese teeth are creamy white in colour. Experiments in the Department of Minerals showed that by soaking one of the Maltese specimens in a solution of ferrous sulphate or iron alum, precipitating the iron as ferric hydroxide, and then treating with tannic acid to produce a blackish tinge the colour of the Piltdown molar could be reproduced exactly.

| | Percentages | | | | | | |
|---|---|---|---|---|---|---|---|
| | N | C | $H_2O$ | $F/P_2O5$ ($\times$ 100) | CaCo$_3$ | Ash | p.p.m. $eU_3$ $O_8$ |
| Dentine of Recent teeth . | $>2$ | $>6$ | $>13$ | $<0·3$ | 5 | $<60$ | $<1$ |
| Piltdown hippo molar dentine | 0·06 | 2 | 12 | 0·3 | 2 | 84 | 3 |
| Ghar Dalam hippo molar ,, | nil | nil | 7 | 0·3 | 14* | 87 | 7 |

* After staining in an iron sulphate solution this was reduced to 5 per cent.

The presence of chromium in the specimens from Piltdown suggests that they were treated with chromic acid or a dichromate solution with the idea of aiding the oxidation of a ferrous staining agent. If an iron sulphate had been used, it might account for one other feature of the composition of the Piltdown *Hippopotamus* molar, namely, the presence of calcium sulphate.

In 1949 an X-ray powder diffraction photograph of the blackened dentine, taken in the Government Chemist's Department, revealed the presence of calcium sulphate. Using the same technique Dr. G. F. Claringbull later detected calcium sulphate (gypsum), apparently partly replacing the calcium phosphate, in several of the bones and teeth from Piltdown. With Dr. M. H. Hey he has shown (p. 268) that the gypsum could be the result of artificial treatment of the specimens, and probably originated through interaction of the calcium phosphate of the bone or dentine and a solution of an acidic iron sulphate.

Tests carried out by Dr. C. Bloomfield of Rothamsted Experimental Station showed that, at the present day, $SO_3$ (sulphate) ions are unusually low in the Piltdown gravel, hence it is not possible to maintain that the sulphate-bearing specimens owe their composition to some natural mineralizing process peculiar to the deposit. No gypsum crystals could be detected by X-ray analysis of the fine fraction of the gravel.

Eventually samples of all the Piltdown mammalian specimens were examined for the presence of chromium, either spectrographically in the Department of the Government Chemist, or chemically in the Department of Minerals of the British Museum, where they were also submitted to X-ray crystallographic analysis (see p. 269).

Several of the results obtained are worth commenting on here. Chromium and gypsum were detected in a premolar of *Hippopotamus* (the first Piltdown fossil shown to Woodward), proving that it too had been artificially stained. This tooth, having a higher fluorine content (1·1%), presumably did not come from the same source as the molar. But both the hippopotamus teeth are less radioactive than any Pleistocene fossils from sand or gravel that have been tested (see Table XI), suggesting that they are from calcareous or argillaceous deposits, for it is known that phosphates are less prone to adsorb uranium where the strata are rich in calcium carbonate or consist largely of clay (Davidson & Atkin, 1953 : 27).

Chromium was also found in the longitudinally split portion of a *Cervus* metatarsal (Dawson & Woodward, 1913 : 121, 142), which had been included in the so-called contemporary group. No sulphate was detected in this bone, indicating that the staining solution used either was not sulphate, or was not sufficiently reactive to cause replacement of the phosphate. A few specimens in the "contemporary" group, including the mandible and incisor of *Castor fiber*, were found to contain calcium sulphate, but no chromium. These were presumably stained by another technique, which dispensed with the use of a dichromate solution as oxidizer.

The fluorine and organic content of the beaver mandible could be matched among bones from either Late Pleistocene or Holocene deposits.

In addition to the artificially stained mandibular fragment and incisor, the Piltdown collection includes two molars of *Castor fiber*. They both show superficial iron-staining which may be artificial. One of the molars was left in its gravel matrix. This seemed to be visible proof that the Piltdown gravel did in fact contain fossils, but on examination the block containing the tooth proved to be an artifact. When soaked in water it began to break down, revealing that it consisted largely of loamy material with a concentration of pebbles on the outside. When the water in which the block had been soaking was evaporated there was a large amount of gummy residue (0·8 gm.). According to its former label one of the pieces of " *Stegodon* " teeth (E.620) was also kept for a time in a similar lump of hardened gravel (see also Dawson & Woodward, 1914 : 84).

One of the fragments of a cream-coloured bone said to have been found *in situ* in clay at the base of the Piltdown gravel (and regarded by Dawson and Woodward as indicating the source of the worked slab of elephant femur) is still embedded in a lump of loam, adhering to the middle of a slab of ironstone. On close examination the loamy matrix shows every indication of being faked. It contains small scattered pebbles set at various angles, and its shows cracks and bells of burst air-bubbles such as appear if loamy matter is worked into a paste and then allowed to set. The sliver of bone embedded in this artificial matrix is identical in composition with the worked elephant bone which, to judge from its state of mineralization and radioactivity, could have been obtained from one of the brickearths in the 50-ft. terrace of the Thames or from an equivalent deposit in the Somme Valley.

| | $\frac{\% F}{\% P_2O_5} \times 100$ | p.p.m. $eU_3O_8$ |
|---|---|---|
| *Elephas* femur (worked), Piltdown | 4·2 | 10 |
| Fragment from " base of gravel," Piltdown | 4·2 | 9 |
| *Cervus* antler, Piltdown | 5·4 | 11 |
| *Elephas* metatarsal, Crayford Brickearth | — | 8 |
| *Rhinoceros* ulna, Crayford Brickearth | 3·5 | — |
| *Elephas* astralagus, Ilford Brickearth | — | 33 |
| *Rhinoceros* astralagus, Menchecourt Sands, Somme | 3·4 | (10)* |

* Estimation based on an associated specimen.

The base of an antler of red deer, *Cervus elephus*, and an upper molar of *Equus* cf. *caballus* (Irving, 1913) were found together in the adjacent field to the west of the gravel pit, " on the surface close to the hedge " (Dawson & Woodward, 1913 : 121). Neither bears any sign of having been rolled on the river bed. In its fluorine content and radioactivity the stag antler is closely comparable with the worked elephant bone. The horse tooth has a much lower fluorine content and shows no radioactivity, indicating that it was derived from a different deposit. The surfaces of both the horse tooth and the stag antler show patchy red iron-staining which recalls in appearance the artificially stained flints (p. 244).

Of the eighteen specimens of fossil mammals recorded from the Piltdown gravel by Dawson and Woodward, ten are unquestionably frauds, and there are strong grounds for believing that this is also true of the remainder. Since the gravel is decalcified (pH 6.5) it is probably unfossiliferous.

# 5. THE COMPOSITION OF THE PILTDOWN HOMINOID REMAINS

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## (1) THE MANDIBLE AND TEETH

THE discovery in the autumn of 1953 that the Piltdown mandible contained the same amount of nitrogen as fresh bone might be regarded as proving its modernity beyond all doubt. In actual fact, however, this would not have been conclusive evidence without the cross-check provided by fluorine analysis. Thus, an ulna of woolly rhinoceros (M.12575) found at a depth of 42 ft. in an Upper Pleistocene river deposit on the site of Lloyd's in the City of London (Warren Dawson, 1925) has a nitrogen content about the same as that of the Piltdown mandible. The reason for the remarkable preservation of the rhinoceros bone is that it was embedded in an unoxidized clay—an environment in which bone-protein decays very much more slowly than in the oxidizing environment of sand or gravel. In marked contrast, a fragment of mammoth femur (M.12946) found at a depth of 20 ft. on the same site, and of the same general age, but preserved in sand, was found to contain very little nitrogen. Fortunately the fluorine content of bone increases at about the same rate in sand (or gravel) and in clay. Thus the fluorine content of the rhinoceros bone is almost the same as that of the mammoth bone.

| | | | % N | % F |
|---|---|---|---|---|
| Upper Pleistocene bones from Lloyd's site | *Rhinoceros*, in clay | *av.* | 3·4 | 1·1 |
| | *Elephas*, in sand | | 0·1 | 1·3 |
| Piltdown mandible, " in gravel " | | | 3·9 | <0·03 |
| Fresh mammalian bone | | | 4·1 | 0·03 |

If the Piltdown mandible had occurred naturally in the shallow Piltdown gravel (early Upper Pleistocene) it should not have contained more nitrogen than the skull bones. Moreover, its *fluorine* content should have been greater than that of fresh bone no matter whether the matrix were clay or gravel.

In one account of finding the mandible Woodward (1948 : 11) wrote : " It had evidently been missed by the workmen because the little patch of gravel in which it occurred was covered with water at the time of year when they reached it." At an early stage in the present investigation it had to be borne in mind that conditions in the Piltdown gravel might have been exceptional and that reducing conditions in the basal bed had preserved collagen in the bone. Through the courtesy of the Director of the Rothamsted Experimental Station the chemical conditions in the Piltdown deposits were recently examined by Dr. C. Bloomfield, who found that the "redox potential" in the basal bed indicated oxidizing, not reducing, conditions.

In March, 1952, Professor J. T. Randall and Dr. A. V. W. Martin undertook to examine the collagen in samples of the teeth by means of the electron-microscope. The first results were inconclusive, for in drilling the samples frictional heat had probably de-natured the collagen. Early this year a new attempt was made to determine the state of collagen in the mandible. A small piece of the bone was sawn out and submitted to Dr. Martin, together with a similar sample of the cranium and other selected controls. Electron-micrographs of the decalcified residue of the mandible sample revealed the presence of fairly well preserved collagen fibres with characteristic banding at intervals of 640 Ångström units (Pl. 30, fig. 11), whereas electron-micrographs of samples of the skull showed no trace of collagen fibres. A residue of the Lloyd's rhinoceros bone also proved to contain collagen fibres, but they were partly de-natured and showed only vague shadows of the original banding. The only fossils in which collagen fibres have been found previously are from frozen ground—see Randall *et al.*, 1952. Collagen is denatured at 70°–100° C.

It has been suggested that collagen fibres may be preserved intact through the action of peat acids, but none was detected in a sample of human bone with undiminished nitrogen content from Holocene peat at Branston, Nottinghamshire, nor in a sample of human skin from the Tollund Bog, Denmark (kindly supplied by Dr. Knud Thorvildsen of the National Museum Copenhagen).

Estimation of the fat content of the mandible, suggested by Heizer & Cook (1954 : 94) as a possible means of confirming its modernity, was considered impracticable with a sample of the limited size available for such a test.

In addition to the nitrogen content, the organic carbon, water and ash contents of the mandible have been determined and compared with those of selected controls. The results confirm that this bone is modern, and also show that such artificial treatment as it received has affected the organic fraction only very slightly.

| | % N | % C | % $H_2O$ | % Ash |
|---|---|---|---|---|
| Modern ungulate limb-bone | (4·0) | 14·0 | 24·5 | (53) |
| ,, ,, ,, 2nd sample | (4·1) | 10·3 | 21·2 | — |
| Piltdown mandible | (3·9) | 14·5 | 25·0 | (61) |
| Piltdown (left parietal) | 1·4 | 6·1 | 17·8 | 62 |
| Neolithic human skull, Coldrum | 1·9 | 6·3 | 18·2 | 71 |
| Lloyd's rhinoceros ulna | 3·4 | 10·4 | 18·9 | (67) |
| Lloyd's mammoth femur | 0·1 | 2·6 | 10·8 | (82) |

*Note.*—The figures in brackets are determinations made on separate samples and therefore independent of other figures on the same line.

The dark mahogany colour of the mandible, matching that of the skull bones very closely, is relatively superficial. Drilling revealed that the interior tissue is buff to pale grey in colour, suggesting that the organic matter filling the pores of the bone prevented the iron-staining solution from penetrating deeply. When the mandible was being drilled with a dental burr to procure an adequate sample for the re-determination of fluorine, there was an odour of burning, and the ejection consisted of minute shavings. When the skull bones were drilled in the same way there was no odour, and the sample consisted of powder.

The mandible shows practically no radioactivity (see Tables X, XII), which is a further confirmation of its modernity.

The fluorine content of the canine and of the molars in the mandibular ramus was estimated in 1949 as $< 0{\cdot}1\%$, but as the mandibular bone itself appeared to contain *c.* 0·2%, and as the probable experimental error on samples of the small size then tested was known to be about ± 0·2% (Oakley & Hoskins, 1950, 379–80), there seemed no reason to regard the canine or the mandible as more recent than the human cranium, with fluorine content estimated to vary from 0·1 to 0·4%. In 1953, new samples of the teeth and of the skull bones were submitted to the Department of the Government Chemist, where Mr. C. F. M. Fryd had devised a technique for estimating smaller amounts of fluorine than could be measured in 1949. The experimental error in the determination of fluorine obviously depends on the size of the sample and the amount of fluorine it contains. The fluorine content of the Piltdown skull bones was determined in 1953 as 0·14 to 0·18%, and the limits of error as ± 0·02%. Where the amount measured was exceptionally small, the fluorine content was recorded as less than 0·0*x*%, the true figure lying between 0·0*x* and zero. In 1953 all the determinations of the fluorine content of the Piltdown mandible and teeth proved to lie between 0·04% and zero. These results indicated that whereas the skull bones were probably prehistoric, the canine tooth, the mandible and the isolated molar were modern. This conclusion was reinforced by comparing the nitrogen content of the Piltdown bones and teeth (dentine) with that of modern and fossil specimens.

In order to eliminate any possibility that the nitrogen found in the dentine samples was not original but due to contamination of the samples, their organic carbon was also determined. The carbon/nitrogen ratio in the molars and in the canine proved to be slightly lower than in the dentine of two modern teeth which were used for comparison, but approximately the same as in the organic matter of bone (2·296 ± 0·266, Cook & Heizer, 1952 : 4).

| | % N | % C | C/N |
|---|---|---|---|
| Modern beaver molar (old individual) | 2·2 | 6·5 | 3·0 |
| Modern orang-utan canine | 3·9 | 12·8 | 3·2 |
| Piltdown canine | 5·1 | 12·1 | 2·3 |
| Molars in Piltdown mandible | 4·3 | 10·0 | 2·3 |
| Isolated Piltdown molar | 4·2 | 10·7 | 2·5 |

In 1950 Dr. David B. Scott of the National Institute of Dental Research, Bethesda (Maryland) undertook to examine collodion replicas of the surfaces of the Piltdown teeth, using the metal-shadowing technique which he has developed with Wyckoff (1946). After examining replicas of the buccal surfaces of the molars in the Piltdown mandible, Dr. Scott reported that " they are not readily recognizable as ancient teeth, since they show very little evidence of post-mortem damage". But, in contrast, replicas of the isolated molar and of the crown of the canine near the tip revealed considerable damage. These findings agree with the results of the present detailed re-examination, that the molars in the mandible have been artificially abraded only on the occlusal surfaces, whereas in the canine and isolated molar the buccal surfaces also have been smoothed artificially.

The black coating on the canine is a paint made from a natural bituminous earth containing iron oxide, probably Vandyke brown (see p. 272). If bituminous matter were not out of place in a highly oxidized gravel it might have been regarded as a natural incrustation. It should also be recorded that Dr. Claringbull found a minute spherule of an iron alloy embedded in the coating on the labial surface of the crown.

The pulp cavity of the canine contains 19 loose sand grains, mostly radio-opaque. Some were extracted for examination and proved to be pellets of limonitic ironstone identical with those which occur in the sand-fraction of the Piltdown gravel. As seen in the radiograph of this tooth (Weiner, Oakley & Le Gros Clark, 1953, pl. 9, fig. 4), all the grains are 1–2 mm. in diameter. If they had been naturally washed into the cavity finer grade material would be expected to have entered with them, for 30% of the grains in the sand-fraction of the Piltdown gravel are *less* than 1 mm. in diameter. The cavity has been sealed by an ovoid grain of hard limonitic ironstone tightly wedged into the aperture of the truncated apex.

## (II) THE PILTDOWN SKULL BONES

As the fluorine and nitrogen content of the cranial bones were consistent with their being fairly ancient, it seemed at first that the hoax had been based on a genuine discovery of portions of a skull in the gravel, and that the animal remains and implements had been subsequently " planted " to suggest that it was Pliocene or Early Pleistocene in age. As the investigations proceeded the skull too became suspect. Dr. G. F. Claringbull carried out an X-ray crystallographic analsyis of these bones and found that their main mineral constituent, hydroxy-apatite, had been partly replaced by gypsum. Studies of the chemical conditions in the Piltdown sub-soil and ground-water showed that such an unusual alteration could not have taken place naturally in the Piltdown gravel. Dr. M. H. Hey then demonstrated that when sub-fossil bones are artificially iron-stained by soaking them in strong iron sulphate solutions this alteration does occur. Thus it is now clear that the cranial bones had been artificially stained to match the gravel, and " planted " at the site with all the other finds. The presence of chromium in some of the bones is now more readily explicable, for a dichromate solution might have served to aid the oxidation of iron salts used in staining the bones.

Since all the " local Upper Pleistocene " fossils with comparable composition have proved to be fraudulent introductions, the low fluorine content of the skull indicates that it is more probably post-Pleistocene than Pleistocene in age.

In 1912, no organic matter could be detected in the small piece of the Piltdown I calvaria submitted for analysis to Mr. S. A. Woodhead, Public Analyst of East Sussex (Dawson & Woodward, 1913 : 121). The specific gravity of the powdered fragment was also measured (2·115) ; but neither of these determinations was significant so long as no comparison was made with the mandible. The first physical comparison between the mandible and the calvaria fragments was recorded in a note dated 1925 by Dr. A. T. Hopwood, who found that their specific gravities, measured *in vacuo*, were as follows:

Mandible 2·06; Piltdown I occipital 2·13; Piltdown II frontal 2·18.

The specific gravities of the Piltdown II occipital and isolated molar have been determined more recently as 2·20 and 2·18 respectively. If allowance is made for the density of the molars, the specific gravity of the bone of the mandible becomes 2·05. The difference between the specific gravity of the mandible and of the calvaria would possibly have been greater if the constituent apatite had not been so extensively replaced by gypsum, which is a lighter mineral, although additional iron oxide may have counterbalanced this effect.

The age of the Piltdown skull has been questioned on the score that it included nasal bones in close association (Marston 1950: 293). Unless ankylosed before death the nasal bones have commonly separated even in recent burials. It was therefore difficult to understand their occurrence together in the upper disturbed layer of the gravel (Dawson & Woodward, 1914: 84). However, there was always the possibility that the nasal bones did not belong to the Piltdown skull. These bones show partial replacement by gypsum, indicating that they were artificially iron-stained. To judge from their composition they were not obtained from the same source as the other cranial fragments. In drilling samples from the nasal bones the ejection consists of shavings (as when the Piltdown mandible was drilled). This is not a proof that a bone is modern, for the property of peeling under the shearing action of a rotating burr is a function of the extent to which the collagen ground-mass of the bone is preserved; and under exceptional conditions this has persisted intact even since Pleistocene times.

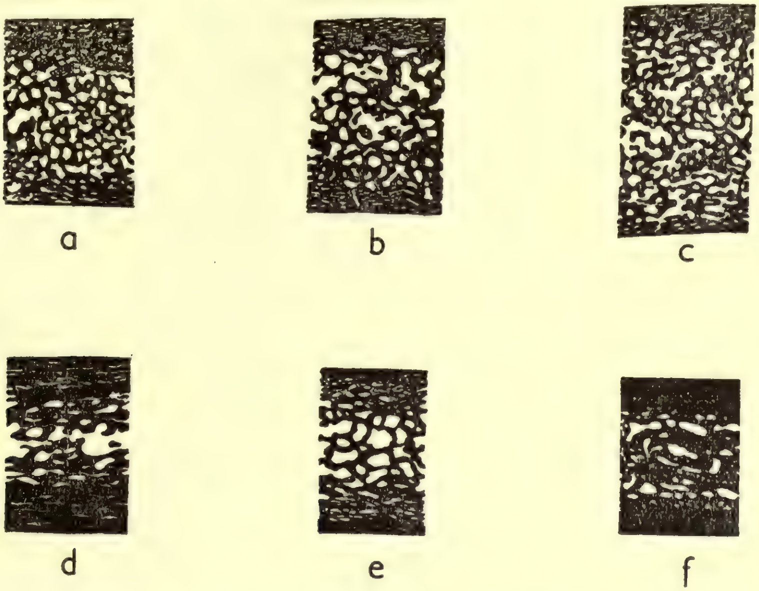
| | Percentages | | | | |
|---|---|---|---|---|---|
| | F | N | C | $H_2O$ | Ash |
| Fresh bone | 0·03 | 4·1 | 14·0 | 25 | 53 |
| Piltdown nasal bone | 0·21 | 3·9 | 20·9 | 27 | 59 |
| Piltdown "turbinal" | 0·28 | 1·7 | 6·1 | 25 | 58 |
| Piltdown I calvaria (*maxima*) | 0·18 | 1·9 | 7·5 | 19 | 76 (*min.* 62) |

Apart from the artificial staining, the Piltdown nasal bones differ from normal fresh bone only in their fluorine content, which is in excess of that found in recently buried skeletons except in areas of endemic fluorosis (Bell & Weir, 1949: 89), or possibly where the soil has been treated with fluorine-rich phosphate fertilisers.

The great thickness of the Piltdown cranial bones is remarkable (e.g. maximum thickness of the parietals 12 mm.), but not unique. Cross-sections of the bones show that the thickness is accounted for by an expansion of the diploe tissues; the inner and outer tables are relatively very thin. In all those palaeolithic skulls with very thick cranial walls that have been examined histologically, the tables are nearly as thick or even thicker than the diploe (Text-fig. 5). In its structure and thickness the Piltdown skull can be matched exactly among some recent crania, for example a skull of an Ona Indian from Tierra del Fuego in the British Museum collection

(1938.8.10.2). However, such skulls are undoubtedly rare, and to find *two* in the same condition at one site would be most unlikely.

The thickening of the diploe in the cranium may be a reflection of a severe chronic anaemia. The late Professor S. G. Shattock, who examined the Piltdown skull from the viewpoint of a pathologist reported (1913 : 46) :



TEXT-FIG. 5. Thin sections of parietal and frontal bones of Piltdown and other human skulls. *a*, Piltdown I, parietal ; *b*, Piltdown II, frontal ; *c*, Ona Indian, parietal ; *d*, Swanscombe, parietal ; *e*, Fontéchevade II, parietal ; *f*, Gibraltar I, parietal ? *a–e* drawn from original specimens ; *f* based on drawing by Shattock (1913). × 3. *del. D. E. Woodall.*

> " Certain details of the Piltdown calvaria . . . suggest the possibility of a pathological process having underlain the thickened condition. These are : (1) The extreme thinness of the tables ; the diploe is closed in on either aspect with the thinnest compact lamina ; such as can be matched . . . [an ancient Egyptian parietal is quoted] where the thickening . . . is incontestably the residue of a morbid process. (2) The presence of the elevated patches on the inner surface of certain of the fragments already detailed : in the modern adult skull such fine vascular furrows as there may have been during growth, on the inner aspect of the tabular bones, have been smoothly filled in. And (3) to this may be added the synostosis which has here and there taken place at the sutures although the age of the individual is approximately only 25 years."

The fragments of the so-called second Piltdown skull have also been artificially stained, for they contain chromium and show partial alteration to gypsum. They comprise a small piece of occipital bone and part of a right frontal of unusual thickness. The occipital fragment is not remarkable in thickness or any other morphological feature, but its neat rectangular outline suggests that it has been trimmed to that shape. The frontal fragment is also rectangular as though broken deliberately. This latter piece could belong to the first cranium, with which it agrees in its exceptional thickness and unusual structure, yet in its total composition it appears to have rather more in common with the occipital fragment grouped with it than with the occipital or other bones of the first skull.

| | Percentages | | | | | | | | p.p.m. |
|---|---|---|---|---|---|---|---|---|---|
| | N | C* | $CaCO_3$ | $P_2O_5$ | $F/P_2O_5$ (× 100) | Fe | $CaSO_4$ | Cr | $eU_3O_8$ |
| Piltdown I : | | | | | | | | | |
| Left fronto-parietal (*av.*) | 1·1 | 6·8 | 3·9 | 18·7 | 0·8 | 6 | + | 1·5 | 3 |
| Left temporal | 0·2 | 4·8 | 3·6 | 23·2 | 0·8 | 8 | ++ | 0·7 | 1 |
| Right parietal | 1·4 | 5·3 | 3·0 | 19·8 | 0·8 | 5 | ++ | 0·0 | <1 |
| Occipital | 0·3 | 6·8 | 4·5 | 20·8 | 0·7 | 6 | ++ | 0·2 | 2 |
| Piltdown II : | | | | | | | | | |
| Right frontal | 1·1 | 4·4 | 1·5 | 14·6 | 0·8 | 10 | ++ | <0·1 | <1 |
| Occipital | 0·6 | 3·9 | 2·0 | 13·6 | 0·2 | 9 | ++ | <0·1 | 0 |

* Carbon in organic fraction.

However, when the analyses are compared, it appears possible that the resemblances between the two fragments of the Piltdown II group are not original but are due to the bones having received the same chemical treatment. The fronto-parietal bone of the Piltdown I group has been less extensively altered to gypsum than the others, and it shows the highest radioactivity, the highest chromium content and the highest carbonate content. The Piltdown II bones, to judge from their high iron, low carbonate and low phosphate content, received a more intensive treatment with an acidic iron salt than any of the Piltdown I bones ; and it seems probable that their lower radioactivity[1], lower chromium content and lower carbon content also reflect differences in treatment.

The feature in the composition of bones which is least likely to be affected by the iron sulphate and chromate treatment is the fluorine/phosphate ratio, and in this the frontal of II agrees with the bones of skull I and not with the occipital which was placed with it.

These more detailed investigations therefore lend further support to the provisional conclusion reached in our 1953 report (p. 145) that the right frontal fragment originally formed part of the first skull. It is probable that the second skull, from which the thinner occipital fragment was obtained, was in a sub-fossil condition similar to that of the first skull.

The human cranial fragments (frontal, parietal and zygomata) reported to have been found by Dawson in gravel of the Piltdown terrace at Barcombe Mills appear to be pieces of two or possibly three skulls. All these fragments have been artificially iron-stained, by the sulphate process, but unaided by a chromium compound. In composition they are broadly comparable with the Piltdown calvaria, but they differ from all the fragments of these, excepting the occipital of Piltdown II, in their thickness and structure, which approximate more closely to the normal.

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[1] It has been suggested that the radioactivity of some of the Piltdown bones may be correlated with traces of $K^{40}$ due to their having been treated with a solution of potassium dichromate. However, direct tests failed to demonstrate any exact correlation between the potassium content of the specimens and either their radioactivity or their chromium content. It is probable that after the bones had been stained some of the potassium ions would have been removed in solution while the chromium ions became fixed.

The possibility that occipital II belonged to one of the " Barcombe Mills " skulls has been considered, but only the parietal agrees in nitrogen content, and this differs in showing a weak radioactivity which may be original since it cannot be attributed to $K^{40}$ in potassium dichromate. In contrast occipital II shows no radioactivity.

## TABLES OF ANALYSES III—VII.

In these tables nitrogen determinations in italics by Mrs. A. Foster, in the Department of Minerals, British Museum (Nat. Hist.), 1953; the remainder of the nitrogen, $H_2O$ and ash determinations by Dr. G. Weiler and Dr. F. B. Strauss in the Microanalytical Laboratory, Oxford, 1954. Inorganic carbonate determined by Mr. C. F. M. Fryd (see p. 266), in the Department of the Government Chemist; organic carbon (C) calculated from his figures and those of Drs. Weiler and Strauss.

Phosphate ($P_2O_5$), fluorine and iron (Fe) determinations in italics by Dr. C. R. Hoskins (1949–51), the remainder of these by Mr. C. F. M. Fryd (1953–4).

The chromium values in italics are spectrographic estimations made in the Department of the Government Chemist; the remainder of the chromium values are chemical determinations by Dr. A. A. Moss in the Department of Minerals, British Museum (Nat. Hist.).

nil = none detected. + some gypsum detected by X-ray diffraction; ++ much gypsum (in excess of 15% $CaSO_4$). $CaCo_3$ estimated on basis of determination of $CO_2$. Uranium content expressed as $U_3O_8$ determined fluorimetrically by Mr. A. D. Baynes-Cope, Department of the Government Chemist, as $eU_3O_8$ estimated on basis of radioactivity measurements by Mr. S. H. U. Bowie and Dr. C. F. Davidson, Atomic Energy Division, Geological Survey.

TABLE III.—*Analyses of Piltdown hominoid bones*

| Register No. | Description | Percentages N | C | $H_2O$ | Ash | $P_2O_5$ | F | $F/P_2O_5$ (× 100) | $CaCO_3$ | $CaSO_4$ | Fe | Cr | p.p.m. $U_3O_8$ | $eU_3O_8$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| E.590a. | Piltdown I, left parietal | 1·9 | 6·1 | 17·8 | 62·4 | — | — | — | 3·6 | + | — | 1·50 | 4 | 3 |
| E.590b. | Piltdown I, left frontal | 0·3 | 7·5 | 19·5 | 72·6 | 18·7 | 0·15 | 0·8 | 4·1 | + | 6 | 1·00 | — | |
| E.591. | Piltdown I, left temporal | 0·2 | 4·8 | 15·8 | 75·3 | 23·2 | 0·18 | 0·8 | 3·6 | ++ | 8 | 0·65 | 4 | 1 |
| E.592. | Piltdown I, right parietal | *1·4* | 5·3 | 19·0 | 68·7 | 19·8 | 0·15 | 0·8 | 3·0 | ++ | 5 | nil | 2 | <1 |
| E.593. | Piltdown I, occipital | 0·3 | 6·8 | 16·7 | 76·1 | — | — | — | 4·5 | 14·4 | — | 0·15 | 8 | 2 |
| | additional fragment | *1·6* | — | — | — | 20·8 | 0·14 | 0·7 | 4·0 | + | 6 | nil | — | — |
| E.594. | Piltdown I, mandible | *3·9* | 14·5 | 25·0 | 60·5 | 20 | <0·03 | <0·2 | 6·5 | 0 | 3 | 0·30 | nil | <1 |
| E.610a. | Piltdown I, nasals | *3·8* | 20·9 | 26·9 | 58·5 | 14·5 | 0·21 | 1·5 | 2·0 | ++ | *c.10* | *nil* | — | <1 |
| E.610b. | Piltdown I, "turbinal" | 1·7 | 6·1 | 24·9 | 58·2 | 16·6 | 0·28 | 1·7 | 1·6 | ++ | *c.15* | *nil* | — | — |
| E.644a. | Barcombe Mills, frontal | 2·4 | 7·3 | 21·5 | 68·5 | 26·5 | 0·07 | 0·3 | 2·2 | ++ | *c.11* | *nil* | — | 1 |
| E.644b. | Barcombe Mills, parietal | 0·3 | 5·0 | 16·1 | 73·0 | 26·0 | 0·10 | 0·4 | 3·0 | + | — | nil | — | 2 |
| E.644c. | Barcombe Mills, zygoma | 1·81 | 6·9 | 22·0 | 62·9 | 13·4 | 0·04 | 0·3 | 1·1 | ++ | — | nil | — | — |
| E.646. | Piltdown II, frontal | *1·1* | 4·4 | 18·8 | 68·2 | 14·6 | 0·11 | 0·8 | 1·5 | ++ | *c.10* | 0·05 | — | <1 |
| E.647. | Piltdown II, occipital | *0·6* | 3·9 | 18·6 | 67·2 | 13·6 | 0·03 | 0·2 | 2·0 | ++ | *c.9* | 0·04 | — | 0 |

TABLE IV.—*Analyses of the Piltdown hominoid teeth.*

| Register No. | Description | Percentages N | C | $H_2O$ | Ash | $P_2O_5$ | F | $F/P_2O_5$ (× 100) | $CaCO_3$ | Fe | Cr |
|---|---|---|---|---|---|---|---|---|---|---|---|
| E.594. | Piltdown I molars, dentine | *4·3* | 10·0 | 21·0 | 67·1 | 26 | <0·04 | <0·2 | 5·5 | trace | — |
| E.611. | Piltdown I canine, dentine | *5·1* | 12·1 | 25·4 | 61·7 | 22 | <0·03 | <0·2 | 5·0 | trace | — |
| E.645. | Barcombe Mills molar, dentine | 2·1 | 7·3 | 16·1 | 73·1 | 26·2 | 0·10 | 0·4 | 6·7 | 0·6 | *nil* |
| E.648. | Piltdown II molar, dentine | *4·2* | 10·7 | 22·6 | 56·8 | 25 | <0·01 | <0·1 | 8·0 | trace | — |

TABLE V.—*Analyses of the Piltdown mammalian bones and teeth*

| | | Percentages | | | | | | | | | | | p.p.m. | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Register No. | Description | N | C | $H_2O$ | Ash | $P_2O_5$ | F | $F/P_2O_5$ (× 100) | $CaCO_3$ | $CaSO_4$ | Fe | Cr | $U_3O_8$ | $eU_3O_8$ |
| E.595. | *Mastodon* cf. *arvernensis* molar, enamel | — | — | — | — | *23* | *1·9* | *8·3* | — | nil | *5* | *nil* | 20 | 11 |
| E.596. | *Elephas*. cf. *planifrons* | | | | | | | | | | | | | |
| | molar { cementum | — | — | — | — | *33* | *2·7* | *8·2* | — | nil | *3* | *c.0·3* | 1000 | 610 |
| | molar { enamel | — | — | — | — | 37·2 | 0·66 | 1·8 | 9·0 | — | *1* | — | — | 520 |
| E.597. | *Elephas*. cf. *planifrons* molar, cementum | — | — | — | — | *34* | *2·5* | *7·4* | — | — | *1* | *<0·05* | 1000 | 530 |
| E.598. | *Hippopotamus* molar, dentine | 0·06 | 2·2 | 11·5 | 83·8 | *37* | *<0·05* | *0·3* | 1·8 | ++ | *3* | *c.1·0* | — | 3 |
| E.599. | *Hippopotamus* premolar, dentine | 0·03 | 2·8 | 11·5 | 78·0 | *29* | *1·1* | *3·8* | 5·7 | + | *5* | *c.2·0* | — | 5 |
| E.600. | *Cervus elaphus* antler | — | — | — | — | *28* | *1·5* | *5·4* | — | nil | *3* | *nil* | — | 11 |
| E.601. | *Cervus*, metatarsal | 0·6 | 4·1 | 13·9 | 77·1 | *27* | *0·1* | *0·4* | 5·6 | nil | *4* | *c.1·5* | — | 6 |
| E.602. | *Equus* molar, dentine | *1·2* | — | — | — | 23·7 | 0·67 | 2·9 | 5 | + | *4* | *nil* | — | 0 |
| E.603. | *Castor* molar, dentine | *2·4* | 6·1 | 15·3 | 71·8 | *30* | *0·4* | *1·3* | 4·5 | nil | *3* | *nil* | — | <1 |
| E.615. | *Elephas* femur, worked | — | — | — | — | *30* | *1·3* | *4·3* | — | nil | *2* | nil | — | 10 |
| E.616. | Bone fragment " from base of gravel." | — | — | — | — | *33* | *1·4* | *4·2* | — | nil | *1* | — | — | — |
| E.617. | Bone fragment " from base of gravel." | — | — | — | — | 26·4 | 1·1 | 4·2 | 8·0 | tr. | 3 | — | — | 9 |
| E.618. | *Castor fiber* incisor, enamel and dentine | — | — | — | — | *27* | *0·1* | *0·4* | — | + | *c.10* | *nil* | — | <1 |
| E.619. | *Castor fiber* mandible | *1·8* | 7·8 | 19·8 | 69·0 | 19·2 | 0·28 | 1·5 | 4·4 | ++ | 6 | *nil* | — | <1 |
| E.620. | *Elephas* cf. *planifrons* | | | | | | | | | | | | | |
| | molar { cementum | 0·02 | 1·5 | 7·2 | 87·3 | *39* | *3·1* | *7·9* | 7·5 | nil | *4* | *<0·1* | 1000 | 1060 |
| | molar { enamel | — | — | — | — | 32·2 | 0·83 | 2·6 | 5·4 | nil | — | — | — | 170 |
| E.621. | *Elephas* cf. *planifrons* molar, enamel | nil | 0·1 | 4·3 | 86·5 | *36* | *0·8* | *2·2* | 4·5 | — | *1* | — | — | — |
| E.622. | *Mastodon* cf. *arvernensis* molar, enamel | — | — | — | — | *36* | *2·3* | *6·4* | — | nil | *4* | *nil* | — | 97 |
| E.623. | *Rhinoceros* cf. *etruscus*, premolar, enamel | — | — | — | — | *24* | *2·0* | *8·3* | — | nil | 6 | *nil* | — | 68 |
| E.1383. | *Cervus* tibia | — | — | — | — | *35* | *<0·1* | *<0·3* | — | nil | *1* | — | — | <1 |
| E.1384. | Caprine molar { enamel | 0·09 | 0·7 | 7·6 | — | *32* | *0·7* | *2·2* | 9·4 | nil | *2* | — | — | 0 |
| | Caprine molar { dentine | — | — | — | — | *12* | *<0·05* | *<0·4* | — | — | — | — | — | — |

TABLE VI.—*Analyses of bones used for comparison*

| Register No. | Age and Locality | Description | Percentages | | | | | | | | | p.p.m. $eU_3O_8$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | N | C | $H_2O$ | Ash | $P_2O_5$ | F | $F/P_2O_5$ (× 100) | $CaCO_3$ | Fe | |
| E.2915. | Recent; Surface, Transvaal | Ungulate limb-bone | 4·0 | 14·0 | 24·5 | 53·3 | — | — | — | 5 | — | — |
| | | Second sample | *4·1* | 10·3 | 23·2 | — | 25·4 | 0·03 | 0·1 | 5 | <0·01 | — |
| E.2912. | Neolithic dolmen, chalky soil, Coldrum, Kent | *Homo sapiens* skull | *1·9* | 6·3 | 18·2 | 70·8 | *23* | *0·3* | *1·3* | 13 | *<0·1* | 1 |
| E.2914. | Mesolithic ?, peaty clay, Branston, Notts | *Homo sapiens* rib | 4·6 | 12·3 | 19·1 | 63·4 | — | — | — | 2 | — | — |
| M.1913. | Mesolithic, sand, Tilbury, Kent | *Homo sapiens* skull | 0·3 | 10·6 | 16·9 | 71·5 | *24* | *1·1* | *4·6* | 7 | *0·5* | — |
| E.1361–2. | Upper Palaeolithic burial ?, sandy gravel, Galley Hill, Swanscombe, Kent | *Homo sapiens* limb-bones | *1·6* | 7·3 | 13·9 | 75·5 | 28·7 | 0·56 | 2·0 | 4·3 | 1 | — |
| E.2709. | Upper Pleistocene or Holocene loam, Halling, Kent | *Homo sapiens* limb-bone | 0·03 | 0·5 | 6·9 | 87·4 | *30·5* | *0·9* | *3·0* | 13·8 | *0·2* | 12 |
| M.17012. | Upper Pleistocene loam, Kingston Hill (?), Surrey | *Homo sapiens* skull | 1·1 | 2·6 | 13·1 | 81·0 | 28·9 | 0·65 | 2·3 | 10·9 | 5 | 3 |
| Cheddar Museum | Upper Pleistocene cave-earth, Gough's Cave, Cheddar | *Rangifer tarandus* mandible | 1·5 | 4·4 | 14·6 | 67·5 | 16·3 | 0·14 | 0·9 | 28·2 | <0·15 | — |
| M.12946. | Upper Pleistocene sand, Lloyd's site, City of London | *Elephas primigenius* femur | 0·1 | 2·6 | 10·8 | 81·6 | *27·5* | *1·3* | *4·7* | 12·7 | 3 | — |
| M.12575. | Upper Pleistocene clay, Lloyd's site, City of London | *Rhinoceros antiquitatis* ulna | 3·4 | 10·4 | 18·9 | 67·1 | *26·0* | *1·1* | *4·2* | 8 | *2* | <1 |
| M.15709. | Middle Pleistocene, Middle Gravels, Barnfield pit, Swanscombe, Kent | *Homo* sp. Skull (occipital) | nil | 3·7 | 11·3 | 85·3 | 27·8 | 1·70 | 6·1 | 8·3 | 1·5 | 27 |
| E.2710. | Middle Pleistocene, Middle Gravels, Barnfield pit, Swanscombe, Kent | Bovine rib | trace | 1·1 | 7·6 | 88·5 | *30* | *2·0* | *6·7* | 7·2 | *1* | 32 |
| M.5137. | Early Upper Pleistocene brickearth (loam), Crayford, Kent | *Rhinoceros* ulna | — | — | — | — | *28·5* | *1·0* | *3·5* | 13 | *0·1* | (8)* |
| N.H.M. Paris | Early Upper Pleistocene sands, Menchecourt, (Somme) | *Rhinoceros* astragalus | — | — | — | — | *35* | *1·2* | *3·4* | — | *<0·5* | (10)* |

* Estimation on an associated bone.

TABLE VII.—*Analyses of teeth used for comparison*

| Register No. | Age and Locality | Description | Percentages | | | | | | | | | p.p.m. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | N | C | $H_2O$ | Ash | $P_2O_5$ | F | $F/P_2O_5$ ×100 | $CaCO_3$ | Fe | $eU_3O_8$ |
| Unreg. | Modern | *Pongo* canine, dentine | 3·9 | 12·8 | 24·0 | 64·3 | — | — | — | 4·5 | — | — |
| Unreg. | Modern | *Pan* molar, enamel | trace | 0·7 | 6·6 | 89·6 | — | — | — | 4·2 | — | — |
| | | *Pan* molar, dentine | 3·2 | — | — | — | 24·7 | <0·06 | <0·3 | 7·0 | <1·0 | — |
| ZD.496A. | Modern, Canada | *Castor canadensis* molar, dentine | 2·2 | 6·5 | 13·6 | 54·5 | — | — | — | 5·0 | — | — |
| M.17016. | Upper Pleistocene loam, Kingston Hill ?, Surrey | *Homo sapiens* molar | 0·3 | — | — | — | — | — | — | — | — | — |
| Cheddar Museum | Upper Pleistocene, Gough's Cave, Cheddar | *Rangifer tarandus* molar, dentine | 1·64 | 4·6 | 13·9 | 69·0 | — | — | — | 26·6 | — | — |
| E.2916. | Lower Pleistocene, Ghar Dalam Cave, Malta | *Hippopotamus* molar, dentine | nil | nil | 7·0 | 87·2 | 34·0 | · ·0·1 | 0·3 | 13·8 | <0·1 | 7 |
| M.17034. | Lower Pleistocene loam, Ichkeul, Tunisia | *Elephas africanavus* (= cf. *planifrons*) | | | | | | | | | | |
| | | enamel | trace | nil | 5·2 | 86·6 | 36·8 | 1·00 | 2·7 | 8·4 | 0·15 | <480 |
| | | dentine | — | — | — | — | 32·0 | 2·7 | 8·4 | 11·4 | 0·8 | 580 |
| M.3776. | Lower Pleistocene, Red Crag (sand), Felixstowe, Suffolk | *Mastodon arvernensis* molar, enamel | — | — | — | — | 33·0 | 1·60 | 4·9 | — | 4 | 38 |
| 43483. | Lower Pleistocene, Red Crag (sand), Suffolk | *Mastodon arvernensis* molar, dentine | 0·07 | — | — | 88·2 | 26·9 | 1·89 | 7·0 | 9·3 | *c.*9 | 46 |
| E.2918. | Lower Pleistocene, Siwalik Beds | *Elephas planifrons* molar, enamel | — | — | — | — | 39·0 | 0·78 | 2·0 | 4 | <0·1 | 45 |
| | | cementum, dentine | — | — | — | — | 36·5 | 2·58 | 7·1 | 9 | 0·1 | 56 |
| M.15647. | Lower Pleistocene, Bain Boulder Bed, Pakistan | *Elephas* cf. *planifrons* | | | | | | | | | | |
| | | enamel | — | — | — | — | 38·1 | 0·54 | 1·4 | 5·8 | <0·1 | 24 |
| | | cementum, dentine | — | — | — | — | 34·8 | 2·55 | 7·3 | 11 | 0·1 | |

# 6. CHEMICAL CHANGES IN BONES: A NOTE ON THE ANALYSES[1]

*By* C. F. M. FRYD

Department of the Government Chemist, London

It is obvious that organic material must undergo changes of a chemical nature during the process of fossilization, and early in the last century Middleton (1844) pointed out that some at least of these changes were not complete in periods which were measurable in geological terms. Carnot (1893) examined the rate of accumulation of fluorine in bones as a measure of age. Results indicated a general trend, influenced so greatly by local variables as to be of no direct value. However, Oakley (1948) suggested that the fluorine content of bones from a limited area, as at Piltdown, or from contiguous sites, could with reservations be used to determine the contemporaneity or otherwise of fossils found in physical association; and since that date experience has accumulated (Oakley & Montagu 1949, Oakley & Hoskins 1950) on the extent to which this principle can be used. Further, this principle is of application whether the change investigated is of an additive nature – such as the incorporation of dissolved fluorine and possibly uranyl ions in the hydroxyapatite or skeletal bone – or degradative – such as the loss of fat (Gangl, 1936) or carbon and nitrogen (e.g. Cook & Heizer, 1952); or even sometimes when it is of a partly physical nature such as the accumulation within the porous structure of the bone of oxides of iron and other metals, calcium carbonate, or other salts.

In the present investigation we in the Department of the Government Chemist have endeavoured to assist in solving the Piltdown problem by determining as accurately as possible on the very small samples available the content of fluorine, phosphate and iron by adaptation of published methods, and chromium and potassium spectographically. The content of $SO_4$ has also been determined on one sample. In addition, carbonates have been determined by the use of an apparatus devised for the purpose (Fryd 1954); the carbonate content is of value both as measure of calcareous infiltration and consequent sealing off of originally porous material, as an indication of pH in past conditions and as a necessary subtraction from the total $CO_2$ obtained in the process of determining organic carbon content. Attempts have been made to determine the fat content of fossil bones by adaptation of published methods, but so far no method of value for samples of a very few milligrams in weight, such as are available from Piltdown material, has emerged. The content of organic carbon has been calculated in this laboratory from a combination of our own figures with those supplied by Drs. Weiler and Strauss of Oxford.

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[1] Published by permission of the Government Chemist.

The water of the bone samples was determined by Drs. Weiler and Strauss in the course of their normal routine of C–H analysis, and not in accordance with the special procedure adopted by Cook & Heizer (1952) which involves preliminary drying at 90° and consequently yields lower values.

The nitrogen content of samples was determined in some cases by Mrs. A. Foster using a modification of the micro-Kjeldahl method devised by her in collaboration with Dr. J. D. H. Wiseman ; and in other cases by Drs. Weiler and Strauss using the Dumas method adapted for small samples.

It is hoped to publish full details of the experimental work carried out in the Government Laboratory elsewhere in the near future (Hoskins & Fryd, 1955).

# 7. THE X-RAY CRYSTALLOGRAPHY OF THE PILTDOWN FOSSILS

*By* G. F. CLARINGBULL AND M. H. HEY

Department of Minerals, British Museum (Natural History)

In order to evaluate a suggested method of fluorine age determination by measurement of changes in the X-ray diffraction pattern of hydroxy-apatite with variation of fluorine content (Niggli, Overweel, & van der Vlerk, 1953) a number of bone samples of varying ages were heated to re-crystallize the apatite. One of these heated samples gave an unidentifiable diffraction pattern and was thus unsuitable for the application of the method. This sample, a drilling from the Piltdown cranium, on examination by X-ray diffraction in the unheated condition, was found to be a mixture of gypsum and apatite. A subsequent examination by the same method of many of the Piltdown specimens (see Table VIII) showed that gypsum was widely distributed in them. Large amounts were found in most specimens except tooth enamels.

With the object of accounting for this unusual occurrence of gypsum in bone, not apparently previously recorded, samples of gravel and loam were collected from the Piltdown site and were examined by chemical and X-ray diffraction methods. A sample of water from a well ¼ mile NE. of the site was also examined for sulphate. The sulphate contents of both water and soil samples, as determined by Dr. Roy C. Hoather and Dr. C. Bloomfield, are notably low.[1] Separation of fine fractions from the loam and gravel samples failed to disclose the presence of sulphate minerals and gave only diffraction patterns of clay minerals and quartz. These results tend, therefore, only to emphasize the anomalous character of the the gypsum in the bone and to rule out its introduction by natural processes. As there was no obvious reason for the intentional introduction of gypsum as such into the supposed fossils it seemed likely that it might have resulted from reaction with a solution used for colouring more recent bones to simulate iron-stained fossils.

An additional line of investigation supported this theory of chemical treatment. Part of a skull from Barcombe Mills in the C. Dawson collection at the British Museum (Nat. Hist.) had some adhering matrix. The skull fragments were found to have a composition similar to that of Piltdown, namely gypsum and apatite,

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[1] Water from the well of the " Piltdown Man " Inn, kindly analysed by Dr. Hoather in the Counties Public Health Laboratory, London, contained 63 parts per million $SO_3$; that from Barcombe Mills 47 parts per million. Dr. C. Bloomfield of the Rothampstead Experimental Station found the $SO_3$ in the fine fraction of the Piltdown gravel to be 3·9 mg. per 100 g.

TABLE VIII.—*X-ray examination of Piltdown specimens*

| Geol. Dept. Reg. No. | X (Film No.) | Nature of specimen | Estimated gypsum content |
|---|---|---|---|
| E.590 | 6346 | Piltdown Skull I, left fronto-parietal | + |
| E.591 | 6343 | ,, ,, I, left temporal | ++ |
| E.592 | 6342 | ,, ,, I, right parietal | ++ |
| E.593 | 6384 | ,, ,, I, occipital | + |
| E.593 | 6481 | ,, ,, I, additional fragment of occipital | + |
| E.594 | 6447 | Piltdown Mandible, bone | |
| E.594 | 6478 | ,, ,, molar | |
| E.595 | 6437 | *Mastodon*, molar | |
| E.596 | 6438 | *Elephas* cf. *planifrons*, molar | |
| E.598 | 6368 | *Hippopotamus*, molar | ++ |
| E.599 | 6439 | ,, premolar | + |
| E.600 | 6369 | *Cervus elaphus*, antler | |
| E.601 | 6364 | ,, ,, metatarsal | |
| E.602 | 6440 | *Equus*, molar | + |
| E.603 | 6448 | *Castor*, molar | |
| E.610a | 6385 | Piltdown Skull I, nasal | ++ |
| E.610b | 6386 | ,, ,, I, turbinal | ++ |
| E.611 | 6477 | ,, Canine | |
| E.615 | 6370 | Worked elephant bone | |
| E.616 | 6367 | Fragment of bone from base of gravel | tr. |
| E.617 | 6389 | ,, ,, ,, ,, ,, ,, ,, | |
| E.618 | 6441 | Castor, incisor | + |
| E.619 | 6345 | ,, mandible | ++ |
| E.620 | 6442 | *Elephas* cf. *planifrons*, molar | |
| E.622 | 6443 | *Mastodon*, molar | |
| E.623 | 6444 | *Rhinoceros*, molar | |
| E.644a | 6387 | Barcombe Mills Skull, frontal | ++ |
| E.644b | 6348 | ,, ,, ,, parietal | + |
| E.644c | 6494 | ,, ,, ,, zygoma | ++ |
| E.646 | 6352 | Piltdown Skull II, frontal | ++ |
| E.647 | 6353 | ,, ,, II, occipital | ++ |
| E.648 | 6445 | ,, ,, II, isolated molar | |
| E.1383 | 6365 | *Cervus*, tibia | |

but the matrix was found to contain calcium and ammonium sulphate, although the fine fractions of freshly coloured gravel from the locality contained no appreciable sulphate and consisted of clay minerals.

The most obvious method of producing a brown iron stain on bone is by simple soaking in a solution of a suitable iron salt. Since gypsum is much more soluble in neutral solutions than is hydroxy-apatite, but is less soluble than the latter in sufficiently acid sulphate solutions, it appeared possible that a fairly acid iron sulphate solution used for staining might at the same time convert part of the bone to gypsum. On general chemical grounds, it seemed possible that there might only be a narrow range of pH within which the solution would be sufficiently acid to convert hydroxy-apatite to gypsum but not too acid to deposit iron oxide and stain the specimens. In fact the range of effective pH seems to be quite wide, at least pH 2·5 to pH 6.

Iron alum (ferric ammonium sulphate) has a distinctly acid reaction and it was expected that strong solutions might effect some conversion to gypsum. Experiments showed that even a solution as weak as 2½% was effective in this direction and at the same time produced fairly full brown colour. Ferrous sulphate and ferrous ammonium sulphate are practically neutral in reaction and would not be expected to produce gypsum so readily, but a few experiments were made with ferrous sulphate. These showed that although it had much less reactivity than iron alum some replacement of apatite by gypsum could be effected. The results of these experiments are given in Table IX; Plate 31 shows the X-ray diffraction photographs.

It seems reasonable to conclude, therefore, that the gypsum in these Piltdown specimens is the result of their treatment with solutions of an iron sulphate. In order to produce a similar replacement of the hydroxy-apatite of buried bone it would appear necessary to postulate a soil composition quite unlike that at Piltdown or indeed anywhere except perhaps in the close proximity of a sulphide ore-body undergoing active weathering.

TABLE IX.—*Artificial iron-staining of bone*

| Expt. Number | Solution used | Treatment | Degree of conversion of apatite to gypsum | Colour after treatment |
|---|---|---|---|---|
| | | WHITE BONE, SUB-FOSSIL (NEOLITHIC SKULL, COLDRUM, KENT) | | |
| A | Saturated iron alum | 36 hr. *ca.* 70°C. | Complete | Yellowish-brown |
| G | ,, ,, ,, | 6 hr. *ca.* 70°C. | Almost complete | Yellowish-brown |
| C | ,, ,, ,, | 48 hr. room temp. | Complete | Off white—unchanged |
| F | ,, ,, ,, | 12 hr. room temp. | Partial | Very pale buff, little change |
| L | 10% iron alum | 96 hr. room temp. then $NH_3$ vapour for 2 hours | Complete | Reddish-brown |
| M | 5% ,, ,, | Ditto | Partial | Light brown |
| N | 2½% ,, ,, | ,, | ,, | Patchy, reddish-brown |
| O | Saturated ferrous sulphate | 24 hr. *ca.* 70°C. | ,, | Variable chocolate brown |
| P | Ditto | 40 hr. room temp. | ,, | Light brown |
| | | FRESH BONE | | |
| 2617 | Saturated iron alum | 9 hr. *ca.* 70°C. | ,, | Pale yellow — little change |

# 8. THE BLACK COATING ON THE PILTDOWN CANINE

*By* A. E. A. WERNER AND R. J. PLESTERS

Research Laboratory, National Gallery

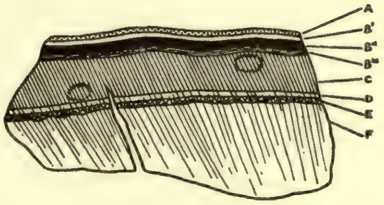
### *Optical examination of cross-section*

In a cross-section of the black coating adhering to a fragment of the root of the canine (Text-fig. 6) the following layers can be distinguished:

(*a*) very thin scattering of a white crystalline material on the surface, thickness *c.* 0·015 mm.; (*b*) three dark brown structureless layers (the middle one almost black) probably comprising the cementum layer of the tooth, *c.* 0·1 mm.; (*c*) stained outer zone of the striated dentine, pale brown semi-transparent, *c.* 0·2 mm.; (*d*) very thin zone of pale yellowish staining, *c* 0·015 mm.; (*e*) thin zone of orange pigmentation, which shows under high power a reticulate structure, *c.* 0·02 mm.; (*f*) white, semi-transparent dentine with characteristic oblique striation.

### *Chemical examination of cross-section*

The zoned appearance of the cross-section suggested that some material from the black coating had been absorbed preferentially through different depths. The surface was treated with organic solvent but little or no solvent effect was noted. It was then treated with dilute hydrochloric acid and a drop of potassium ferrocyanide solution. Excess was washed off with distilled water. The top layers showed a dense mass of Prussian blue, but the pale brown zone below remained unchanged (except where the precipitate had floated into the cavities). Zone *d* was coloured a pale green. Zone *e* was dark blue and Prussian blue penetrated along the striations into the unstained dentine (*f*).



TEXT-FIG. 6. Thin-section of a fragment of the root of the Piltdown canine, showing the zones of staining. × 30 (approx.).

### *Chemical examination of scrapings of the black coating*

Under the microscope the scrapings appeared as deep golden brown translucent lumps ; it was difficult to distinguish between pigment and medium, but a few reddish brown pigment particles were visible. The usual resin solvents—acetone, ethyl alcohol, benzene, chloroform—only extracted a small quantity of material from the sample. The thin cloudy ring of extracted material fluoresced faintly in ultra-violet light. After evaporation of the solvent, the sample itself was left as a hard intact mass. (Paint having an oil-resin medium often behaves in this way, a little of the resin being extracted by organic solvents, yet the paint film itself remaining apparently unchanged. Bituminous surface coatings also behave in a similar manner, a little transparent material being extracted by such solvents). Aqueous ammonia had a slight solvent effect, and alcoholic ammonia slightly greater. Morpholine and alcoholic sodium hydroxide softened and gradually disintegrated the sample. The golden brown transparent material remained dissolved completely in concentrated hydrochloric acid giving a yellow solution. This solution gave a copious precipitate of Prussian blue with potassium ferrocyanide, and a strong red coloration with ammonium thiocyanate. It must therefore contain ferric iron. From the appearance and solubility of the material this would seem to indicate the presence of a transparent iron-oxide pigment.

Further scrapings were heated in a small combustion tube. Heavy brownish fumes with a tarry smell were evolved, and condensed in the form of brown droplets. This suggested the presence of some bituminous material and would also be consistent with the behaviour of the scrapings to solvents. The incombustible residue dissolved in concentrated hydrochloric acid, and gave very strong positive reaction for iron ($Fe^{+++}$).

### *Conclusions*

The black coating contains a considerable amount of a transparent brown iron-oxide pigment; it contains some organic matter which seems to be of a bituminous nature ; and the solubility tests do not exclude the presence of a little oil and/or resin. It therefore seems that the black coating is a paint consisting of a natural bituminous pigment, such as Cassel Earth or Cologne Earth (Vandyke brown), which contains a fairly high proportion of iron oxide, rather than a pure iron oxide pigment mixed with bitumen. The crackle pattern of the paint and its tough, non-brittle character (as examined on the tooth itself) are consistent with the above findings, and would suggest moreover that the surface coating is not of a very great age.

# 9. THE GEOLOGY OF THE PILTDOWN NEIGHBOURHOOD[1]

*By* F. H. EDMUNDS

Geological Survey of Great Britain

THE geology of the Piltdown neighbourhood was described by Charles Dawson in the introduction to his joint paper with Smith Woodward on the Piltdown Skull (1913 : 117). No geological survey of the superficial deposits of the area had then been published. In 1925 the writer, in the course of his official work on the Geological Survey of Great Britain, mapped the superficial deposits of a large area around Lewes on the scale of 6 in. to the mile. The spread of gravel which according to Dawson yielded the Piltdown Skull and other fossils was included in this area.

The Piltdown gravel spread rests on the Tunbridge Wells Sand formation. It measures but 75 yd. × 270 yd. and is one of a number of fragments of a well-defined but much dissected and denuded river terrace which borders the River Ouse. This terrace constantly maintains a height of about 50 ft. above the river, and the Piltdown spread itself is no exception. The 100-ft. contour of the 6-in. Ordnance Survey maps, Sussex 40 NW. and NE. (1911 and later editions), actually crosses the gravel spread, while the 50-ft. contour almost touches the River Ouse at Gold Bridge, the nearest point of the river. This is shown on the accompanying sketch-map.

The obvious correlation is with the 50-ft. terraces of the Thames and other English rivers ; that is, the gravel is of Upper Pleistocene age.

In 1925 there were some two feet of brickearth lying on an equivalent thickness of gravel, which rested on Tunbridge Wells Sand. The gravel was seen to be light brown to orange-red in colour, and to consist largely of sand, with small waterborne pieces of ferruginous sandstone and ochreous flints. Many of the flints were pitted with round or pentangular spaces. The brickearth appears to be water deposited, and to be only slightly later in age than the gravel. It may or may not be contemporaneous with extensive brickearth deposits of Upper Pleistocene age in Kent, some of which have been equated with the loess of Europe. It is of insufficient importance for separate distinction on the Geological Survey map.

Not unexpectedly the detailed survey of 1925 differs in certain particulars from Dawson's account of 1913. This is particularly the case in the matter of height of the gravel spread above the river. Dawson estimated this at about 80 ft. Unfortunately, Sollas (1924 : 183) accepted Dawson's figure without question and equated the terrace with those at about 100 ft. (or 30 metres) above other rivers of Great Britain and Europe. Previous attention has been drawn to this false correlation (Edmunds, 1950).

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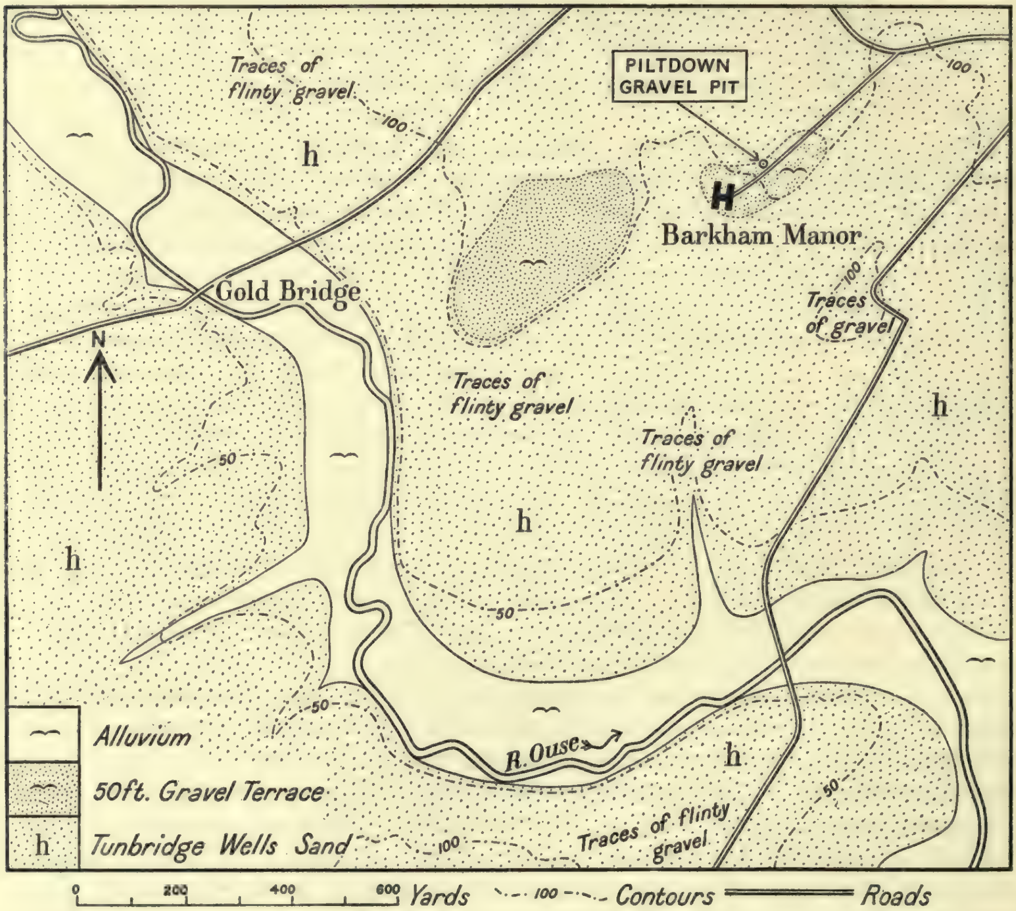
[1] Communicated by permission of the Director, Geological Survey and Museum.

The Geological Survey memoir on the Lewes district (White 1926 : 63) repeats Dawson's estimate in the text. The present writer contributed a text-figure to this memoir (White 1926, fig. 10) indicating the true elevation of the terrace. The significance of this diagram, however, does not seem to have been fully appreciated by Osborne White and the memoir shows a discordance between the text and the diagram.


Traces of flinty gravel
100
h
PILTDOWN GRAVEL PIT
H
Barkham Manor
100
Traces of gravel
Gold Bridge
N
Traces of flinty gravel
Traces of flinty gravel
h
50
h
50
h
50
R. Ouse
h
50
Traces of flinty gravel
100
~ Alluvium
50ft. Gravel Terrace
h Tunbridge Wells Sand
0 200 400 600 Yards
100 Contours
Roads

TEXT-FIG. 7. Geological sketch map of the Piltdown district.

In his 1913 account, Dawson records that the gravel occurred a few inches beneath the surface of the soil, and varied in thickness from 3 to 5 ft. In a supplementary paper (Dawson & Woodward 1914 : 82) he elaborates his description of the gravel section, to say that beneath the surface soil there occurs a bed of undisturbed gravel, from a few inches to 3 ft. in thickness which (he records) overlies a third bed, which though not always present, is well marked, and consists of pieces of ironstone and deeply patinated and iron-stained flints.

The supplementary paper also contains a furthur version of the section in the form of a drawing annotated as follows :

> 1. Surface soil, with occasional iron-stained subangular flints . . . Thickness = 1 foot.
>
> 2. Pale-yellow sandy loam, with small lenticular patches of dark ironstone gravel and iron-stained subangular flints . . . Thickness = 2 feet 6 inches.
>
> 3. Dark-brown ferruginous gravel, with subangular flints and tabular ironstone floor covered with depressions. 18 inches.
>
> 4. Pale-yellow finely-divided clay and sand, forming a mud reconstructed from the underlying strata. Certain subangular flints occur, bigger than those of the overlying beds. Thickness, 8 inches.
>
> 5. Undisturbed strata of the Tunbridge Wells Sand (Hastings Beds, Wealden).

(The indicated omissions from the above annotations concern fossils and flint implements).

This latter description accords reasonably well with the writer's observations made in 1925, and with a photograph of the section in Dawson's 1913 paper which shows what is obviously brickearth, about 2 ft. thick, overlying a similar thickness of gravel.

Traces of the 50 ft. terrace, in the form of *remanié* flints and sandstone in the surface soil are visible over much of the countryside bordering the River Ouse. They have not been noted above the general level of this terrace.

No great significance is to be attached to the mere presence of flints within the Weald. Dark-stained flints occur at many localities and on present-day views of the denudation of the Weald their presence is to be expected. Flints occur, however, in greater numbers in the Piltdown area than have been noted in other districts on the outcrops of the Weald Clay and earlier formations.

It is reasonable to assume that some older drift deposits may have formerly existed at higher levels in the Piltdown district. During Pleistocene times, however, denudation had been so extensive that no field evidence of any earlier drifts remains. The possible former presence above the 50-ft. terrace level of a local drift of any age can only be hypothetical.

# 10. THE RADIOACTIVITY OF THE PILTDOWN FOSSILS[1]

*By* S. H. U. BOWIE AND C. F. DAVIDSON

**Atomic Energy Division, Geological Survey of Great Britain**

DURING recent investigations into the geochemical distribution of the radioactive elements, it was demonstrated by the Atomic Energy Division of the Geological Survey that fossil bones, teeth and other phosphatic materials tend to accrete uranium by adsorption from percolating groundwaters (Davidson & Atkin, 1953). There is some evidence that the radioactivity of a fossil bone is dependent upon the geological age of the fossil, upon the permeability of the formation in which it is found, and upon the uranium content of the percolating waters throughout the ages. In favourable circumstances the determination of radioactivity should therefore provide a means of distinguishing older, derived fossils from contemporary bones when vertebrate remains of more then one age are found in the same geological environment. No intensive research on this topic has yet been undertaken since such academic studies are rather far removed from the Atomic Energy Division's primary function of finding workable uranium deposits.

The build-up of radioactivity in older bones is due to two separate and unrelated causes—firstly, to the longer time that these fossils have had to adsorb uranium from circulating waters and, secondly, to the increase in radioactivity as this uranium approaches secular equilibrium with its daughter elements. The adsorbed uranium has at first only about one-third of the beta radioactivity of uranium in equilibrium with its daughter elements, and the content of the latter disintegration products does not reach a maximum until equilibrium is reached—i.e. until the amount of each transitory daughter element newly generated in a given time is equal to the amount lost by decay. If uranium were present in the bone in a known amount when it was buried, and were not added to or leached away throughout its later history, the radioactivity would gradually increase for a period of several hundred thousand years, and the absolute age could be deduced therefrom. Since, however, the uranium slowly accretes after burial the radioactivity measurements can be no more than a relative indication of age between different bones found in the same geological environment.

When *The Solution of the Piltdown Problem* was published we suggested to the Keeper of Geology that radioactivity measurements might yield additional information on the relative ages of the fossils. He thereupon made a large number of bones and teeth available for radiometric assays, the results of which are reported in this note.

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[1] Communicated by permission of the Director, Geological Survey and Museum.

The study of phosphatic materials by autoradiographic techniques (Bowie, 1951) has shown that in radioactive bones, teeth and apatite crystals the radioactivity may be concentrated towards the surface of the specimen if the latter is relatively impermeable, but if the material is porous the adsorbed uranium tends to become evenly distributed throughout. Both for this reason, and because of the high sensitivity intrinsic to the method, the radiometric analyses of the Piltdown specimens have been conducted by measurement of the beta radiation emitted from the surface of the bone, this radiation emanating from a layer about 5 mm. in thickness. The technique employs a sensitive beta counter, with a thin mica end-window placed at a fixed distance (1 cm.) from the fossil under study, the assemblage being contained in a lead chamber to reduce extraneous radiation to a minimum, and connected to a scaling unit. One great advantage of the method is that it does not consume any of the fossil material, which is preserved unchanged. A disadvantage, with the equipment at present available to us, is that the specimens must be small enough (less than six inches in length) to permit their introduction into the lead chamber, and large enough (about a half-inch minimum diameter) to cover the sensitive area of the end-window counter.

Because of the variation in background count due mainly to fluctuations in cosmic radiation, the accuracy of the measurements (which is a function of the total counts recorded) depends upon the length of time allowed for the determinations. The radioactivity of a relatively uranium-rich bone can be determined with reasonable precision in a few minutes, but specimens in which the radioactivity is very feeble demand an investigation lasting one or two days. In the table below a " standard error " is given, this being a statistical expression of the standard deviation of the background count relative to the count given by the specimen plus background. It will be observed that in certain instances the standard error exceeds the count rate, the relevant specimens being devoid of any radioactivity determinable under these experimental conditions.

From the net count per minute given by each specimen, by extrapolation from analysed standards, the radioactivity has been expressed as equivalent urania ($e.U_3O_8$). This is a measurement of the true (chemical) uranium content only if the radioactive elements are in secular equilibrium and if no radioactive elements other than those of the uranium series are present. In all such phosphatic materials hitherto analysed chemically, no elements of the thorium series have been found in significant amounts ; but in the Piltdown specimens which have reputedly been treated with potassium chromate, part or all of the radioactivity may be due to the potassium isotope $K^{40}$ if the potash salts have not been thoroughly washed out from the bone structure. One per cent. $K_2O$ has a beta radioactivity equivalent to about 0·0007% $U_3O_8$.

Since we have no personal knowledge of the history or provenance of the Piltdown and other specimens submitted to us, it is not appropriate that we should attempt to interpret the results of these tests. There is a strong suggestion that the radioactivity of the bones varies sympathetically with the fluorine content, particulars of which have already been published by Oakley ; but since in relatively young fossil bones the adsorbed uranium cannot have reached secular equilibrium, for such materials radioactive measurements may be less satisfactory than fluorine determinations as pointers to age. Possibly, however, radiometric assays may be of greater value than fluorine determinations for older fossils. It should be noted that the dentine and cementum of teeth is nearly always more radioactive than the enamel (Pl. 30, fig. 13).

The analyses which we have obtained on a group of late Tertiary and Quaternary bones, listed below, suggest a rough correlation of radioactivity with age. Although there are too many variables governing the adsorption of uranium into such materials for radioactivity measurements in themselves to form a reliable means of dating the fossils, radiometric determinations seem likely to provide the palaeontologist with information which, considered in conjunction with other evidence, may be an important help in discerning the relative age of two or more groups of vertebrate remains found in the same geological environment.

TABLE X.—*Radiometric assays of Piltdown specimens*

| Register No. | Locality | Description | Net counts per minute | Standard error | Per cent. $eU_3O_8$ |
|---|---|---|---|---|---|
| E.620 | Piltdown | *Elephas* cf. *planifrons* molar cementum | 354·5 | ±6.0 | 0·106 |
| | | enamel | 57·5 | ±1·2 | 0·017 |
| E.596 | ,, | *Elephas* cf. *planifrons* molar— | | | |
| | | cementum | 203·3 | ±3·2 | 0·061 |
| | | cementum and enamel | 197·2 | ±3·1 | 0·059 |
| | | enamel | 172·6 | ±2·3 | 0·052 |
| E.597 | ,, | *Elephas* cf. *planifrons* molar cementum | 175·2 | ±2·6 | 0·053 |
| | | enamel | 72·8 | ±2·4 | 0·022 |
| E.622 | ,, | *Mastodon* cf. *arvernensis* molar, enamel | 32·4 | ±0·6 | 0·0097 |
| E.623 | ,, | *Rhinoceros* cf. *etruscus* premolar, enamel | 22·8 | ±0·6 | 0·0068 |
| E.595 | ,, | *Mastodon* cf. *arvernensis* molar, enamel | 3·62 | ±0·32 | 0·0011 |
| E.600 | ,, | *Cervus elaphus* antler | 3·57 | ±0·35 | 0·0011 |
| E.615 | ,, | *Elephas* femur (worked) | 3·50 | ±0·32 | 0·0010 |
| E.617 | ,, | Bone in clay matrix, " from base of Piltdown Gravel " | 3·05 | ±0·14 | 0·0009 |
| *E.604 | ,, | *Castor* molar in gravel matrix | 2·50 | ±0·27 | 0·0007 |
| E.601 | ,, | Cervid metatarsal | 2·07 | ±0·32 | 0·0006 |
| E.599 | ,, | *Hippopotamus* premolar, dentine and enamel | 1·79 | ±0·41 | 0·0005 |
| E.598 | ,, | *Hippopotamus* molar dentine | 1·10 | ±0·37 | 0·0003 |
| | | enamel | −0·11 | ±0·33 | <0·0001 |
| E.590 | ,, | *Eoanthropus I*, left fronto-parietal | 0·91 | ±0·11 | 0·0003 |
| E.593 | Piltdown | *Eoanthropus* I occipital | 0·76 | ±0·10 | 0·0002 |
| E.644b | Barcombe Mills | *Homo* parietal fragment | 0·69 | ±0·13 | 0·0002 |
| E.591 | Piltdown | *Eoanthropus* temporal | 0·42 | ±0·11 | 0·0001 |
| E.644a | Barcombe Mills | *Homo* frontal | 0·34 | ±0·12 | 0·0001 |
| *E.603 | Piltdown | *Castor* molar, enamel | 0·30 | ±0·29 | <0·0001 |
| E.1383 | ,, | *Cervus* tibia | 0·25 | ±0·29 | <0·0001 |
| E.619 | ,, | *Castor* mandible | 0·20 | ±0·26 | <0·0001 |
| E.592 | ,, | *Eoanthropus* I right parietal | 0·14 | ±0·12 | <0·0001 |
| E.594 | ,, | *Eoanthropus* I mandibular ramus | 0·05 | ±0·11 | <0·0001 |
| *E.610a | ,, | *Eoanthropus* I nasals | 0·03 | ±0·11 | <0·0001 |
| E.646 | ,, | *Eoanthropus* II frontal | 0·02 | ±0·13 | <0·0001 |
| *E.618 | ,, | *Castor* incisor enamel | −0·05 | ±0·38 | <0·0001 |
| E.647 | ,, | *Eoanthropus* II occipital | −0·14 | ±0·14 | <0·0001 |
| E.1384 | ,, | Caprine molar, enamel | −0·21 | ±0·28 | <0·0001 |
| E.602 | ,, | *Equus* molar, mainly enamel | −0·25 | ±0·38 | <0·0001 |

* Specimens either too small to cover area of end window of counter or not thick enough to be considered deep sources of beta activity. The relative values for these may be up to 50% higher than quoted.

TABLE XI.—*Radiometric assays of various Tertiary, Pleistocene and Holocene Fossils*

| Register No. | Locality and age of stratum | Description | Net counts per minute | Standard error | Per cent. $eU_3O_8$ |
|---|---|---|---|---|---|
| M.17034 | Ichkeul, Tunisia, Lower Pleistocene (Lower Villafranchian) | *Archidiskodon africanavus* (=*Elephas* cf. *planifrons*) | | | |
| | | molar, cementum | 194·9 | ±1·2 | 0·058 |
| | | cementum and enamel | 175·0 | ±1·1 | 0·052 |
| | | cementum, dentine and enamel | 158·6 | ±1·1 | 0·048 |
| 33189 | Touraine, Miocene | *Mastodon* molar, enamel | 114·5 | ±2·5 | 0·034 |
| 15785 | Siwalik Hills, " Lower Pliocene " | Ruminant molar, mainly dentine | 86·8 | ±3·1 | 0·026 |
| | | Ruminant molar, enamel | 49·1 | ±1·3 | 0·015 |
| 32543 | Touraine, Miocene | *Mastodon* molar, enamel | 50·9 | ±1·3 | 0·015 |
| M.10436 | Portslade, Brighton, Pleistocene | *Ursus* cf. *arvernensis* molar— | | | |
| | | dentine and enamel | 27·51 | ±0·49 | 0·0082 |
| | | enamel | 3·69 | ±0·35 | 0·0011 |
| 28804 | Val d'Arno, Lower Pleistocene | *Rhinoceros etruscus* molar— | | | |
| | | osteodentine | 26·0 | ±0·6 | 0·0078 |
| | | enamel | 7·06 | ±0·56 | 0·0021 |
| Buxton Museum | Doveholes, Derbyshire, Lower Pleistocene fissure deposit | *Mastodon* cf. *arvernensis* molar— | | | |
| | | dentine | 25·15 | ±0·37 | 0·0075 |
| | | enamel | 3·85 | ±0·36 | 0·0012 |
| M.11514 | Herbolzheim, Baden, Upper Pliocene fissure deposit | *Mastodon arvernensis* molar— | | | |
| | | dentine | 22·0 | ±0·6 | 0·0066 |
| | | enamel | 6·86 | ±0·36 | 0·0021 |
| E.2918 | Siwalik Hills, Lower Pleistocene | *Elephas planifrons* molar— | | | |
| | | dentine or cementum and enamel | 18·70 | ±0·6 | 0·0056 |
| | | enamel | 14·89 | ±0·50 | 0·0045 |
| E.2691 | Ain Boucherit, Algeria, Lower Pleistocene (Lower Villafranchian) | *Archidiskodon africanavus* (= *Elephas* cf. *planifrons*) molar, dentine | 18·06 | ±0·52 | 0·0054 |
| 43483 | Suffolk, Red Crag, Lower Pleistocene | *Mastodon* cf. *arvernensis* molar | | | |
| | | mainly dentine | 15·44 | ±0·45 | 0·0046 |
| | | mainly enamel | 4·44 | ±0·40 | 0·0013 |
| M.14959 | Senèze (Haute-Loire), Lower Pleistocene | *Equus robustus* premolar, dentine and enamel | 15·40 | ±0·49 | 0·0046 |
| E.2706 | Dovercourt, Essex, Red Crag, Lower Pleistocene | Rolled fragment, compact bone | 15·38 | ±0·42 | 0·0046 |

| Register No. | Locality and age of stratum | Description | Net counts per minute | Standard error | Per cent $eU_3O_8$ |
|---|---|---|---|---|---|
| M.17033 | Ain Hanech, Algeria, Lower Pleistocene (Upper Villafranchian) | *Elephas* cf. *meridionalis* molar—cementum and enamel | 15·07 | ±0·30 | 0·0045 |
| E.2707 | Swanscombe, Lower Gravel, Middle Pleistocene | Ungulate limb-bone | 13·90 | ±0·51 | 0·0042 |
| G.S.M. 3340 | Suffolk, Red Crag, Lower Pleistocene | *Mastodon arvernensis* molar— | | | |
| | | dentine | 13·05 | ±0·43 | 0·0039 |
| | | enamel | 4·15 | ±0·13 | 0·0012 |
| G.S.M. 6838 | Suffolk, Red Crag, Lower Pleistocene | *Mastodon* molar mainly dentine | 12·84 | ±0·25 | 0·0038 |
| | | enamel | 6·77 | ±0·32 | 0·0020 |
| M.3776 | Suffolk, Red Crag, Lower Pleistocene | *Mastodon* cf. *arvernensis* molar, mainly enamel | 12·72 | ±0·38 | 0·0038 |
| 93223 | Ilford, Brickearth, Upper or Middle Pleistocene | *Elephas primigenius* right astragalus | 10·90 | ±0·50 | 0·0033 |
| E.2710 | Swanscombe, Middle Gravels, Middle Pleistocene | Bovine rib | 10·80 | ±0·16 | 0·0032 |
| M.15709 | Swanscombe, Middle Gravels, Middle Pleistocene | *Homo* occipital | 9·03 | ±0·13 | 0·0027 |
| York Museum 1/10-1-74 | Trimley, Suffolk, Red Crag, Lower Pleistocene | *Elephas* cf. *planifrons* molar, cementum, dentine and enamel | 8·87 | ±0·14 | 0·0027 |
| M.15647 | Bain Boulder Bed, India, Lower Pleistocene | *Elephas* cf. *planifrons* molar, cementum and enamel | 7·86 | ±0·42 | 0·0024 |
| York Museum 1a/10-1-74 | Trimley, Suffolk, Red Crag, Lower Pleistocene | *Elephas* cf. *planifrons* molar, mainly enamel with some dentine or cementum | 5·87 | ±0·33 | 0·0018 |
| G.S.M. 93224 | W. Wittering, "Holocene" (Pleistocene ?) | Bovid phalange | 5·70 | ±0·30 | 0·0017 |
| E.2709 | Swanscombe (Ebbsfleet), Upper Pleistocene | Ungulate limb-bone | 4·93 | ±0·28 | 0·0015 |
| E.2705 | Chagny-Bellecroix (Saône-et-Loire), Lower Pleistocene | *Elephas* cf. *planifrons*, fragments of dentine | 4·78 | ±0·44 | 0·0014 |
| G.S.M. C.43 | Ilford, Brickearth, Middle or Upper Pleistocene | *Elephas antiquus* molar, dentine, cementum and enamel | 4·17 | ±0·35 | 0·0013 |

TABLE XI.—*Radiometric assays of various Tertiary, Pleistocene and Holocene Fossils*—(Contd.)

| Register No. | Locality and age of stratum | Description | Net counts per minute | Standard error | Per cent. $eU_3O_8$ |
|---|---|---|---|---|---|
| E.2709 | Halling, Upper Pleistocene? | *Homo* limb-bone | 4·03 | ±0·30 | 0·0012 |
| G.S.M. 5548 | Great Yeldham, Essex, Middle Pleistocene | *Bos primigenius* molar— | | | |
| | | enamel | 3·13 | ±0·39 | 0·0009 |
| | | enamel and dentine | 2·97 | ±0·31 | 0·0009 |
| G.S.M. 3063 | Crayford, Brickearth, Upper Pleistocene | *Elephas* cf. *primigenius* metatarsal | 2·77 | ±0·31 | 0·0008 |
| G.S.M. 10284 | Clapham, Bedford, Upper Pleistocene | *Elephas primigenius* molar, mainly enamel | 2·60 | ±0·18 | 0·0008 |
| E.2916 | Ghar Dalam Cave, Malta, Lower Pleistocene | *Hippopotamus* molar— | | | |
| | | enamel and dentine | 2·41 | ±0·41 | 0·0007 |
| | | enamel | 1·75 | ±0·30 | 0·0005 |
| Brighton Museum G.6480 | Portslade, Upper Pleistocene | *Elephas primigenius* molar— | | | |
| | | cementum | 2·21 | ±0·24 | 0·0006 |
| | | enamel | −0·15 | ±0·22 | <0·0001 |
| 40838 | Urals, U.S.S.R., Lower Pleistocene | *Elephas meridionalis* molar, cementum or dentine | 1·67 | ±0·41 | 0·0005 |
| Zieriksee Museum | Scheldt Estuary, Lower Pleistocene | *Elephas* cf. *planifrons* molar, mainly enamel | 0·41 | ±0·12 | 0·0001 |
| G.S.M. 93225 | Hastings, kitchen midden | *Cervus elaphus* astragalus | 0·23 | ±0·30 | 0·0001 |
| ZD.1938 | Terra del Fuego, Modern | *Homo sapiens* parietal | 0·07 | ±0·12 | <0·0001 |
| *M.12575 | Lloyd's site, London, Upper Pleistocene | *Rhinoceros antiquitatis* ulna | 0·03 | ±0·28 | <0·0001 |
| G.S.M. 5081 | Twickenham, Thames Gravel, Holocene | *Sus scrofa* mandible | −0·29 | ±0·45 | <0·0001 |
| G.S.M. G.S.405 | Hythe, Kent, Holocene | *Sus scrofa* mandible | −0·60 | ±0·42 | 0·0001 |
| G.S.M. 5086 | Twickenham, Thames Gravel, Holocene | *Capreolus capreolus* innominate | −0·68 | ±0·45 | <0.0001 |
| — | Kent, Modern | *Meles meles* frontal | −0·92 | ±0·28 | <0·0001 |

* See footnote to Table X.

# II. THE FLUORIMETRIC DETERMINATION OF URANIUM IN THE PILTDOWN FOSSILS[1]

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IN 1950 Dr. K. P. Oakley asked Dr. C. R. Hoskins of the Department of the Government Chemist to investigate the estimation of uranium in fossil bones, for use as a dating element to supplement the fluorine method.[2]

Dr. Hoskins' preliminary work showed that chemical methods were not sufficiently sensitive for the extremely small samples available, and that a sensitive fluorimeter was necessary. The Chemical Research Laboratory had developed two methods for the isolation of uranium (see *Chemical Methods for the Detection of Uranium,* Stationery Office, London, 1950 ; and U.S. Geol. Surv. Circular No. 199). One, involving chromatographic separation on a cellulose powder column was found to be useless for the samples being examined. The other, using solvent extraction into ethyl acetate, seemed to be adaptable to the estimation of uranium in small samples, and Mr. R. A. Wells of the Chemical Research Laboratory kindly gave instruction in the technique used.

The method finally adopted was as follows :

A sample of bone (2 to 10 mg.) was weighed into a Pyrex tube (13 cm. × 0·75 cm. I.D., with a B.10 stopper) and refluxed with 0·2 ml. of conc. nitric acid until solution appeared to be complete. After cooling, saturated aluminium nitrate (0·5 ml. of a solution in 1% nitric acid), 0·5 ml. of water and 1·5 ml. of carefully purified ethyl acetate were added. The mixture was shaken and after settling, 1·0 ml. of the ethyl acetate was pipetted on to 0·7 gm. of sodium fluoride. The solvent was evaporated, the sodium fluoride dried under infra-red lamps, and finally fused. The amount of uranium was measured in the fluorimeter.

Factors limiting the accuracy of the results were :

(1) Weighing was to the nearest 0·1 mg. only.

(2) The conversion factor from scale reading to uranium content was empirical.

(3) The lowest readings did not differ enough from the background readings to admit of satisfactory determination.

(4) Fluctuation in the meter readings allowed only estimation of the second significant figure.

(5) The carry over of the multiranger was not accurate at the ends of the scale, and errors of 20% could occur.

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[1] Published by permission of the Government Chemist.

[2] The request was inspired by information received from Dr. C. F. Davidson and Professor Harrison Brown. K.P.O.

Taking these factors into consideration only one significant figure can be given for the uranium percentage.

The uranium adsorbed in bone has been shown by Davidson & Atkin (1953) to be concentrated in the surface layers and along cracks and crevices, not necessarily uniformly over any area. A "fair sample" of the bone for analysis must, then, have a representative proportion of the outer layer to the inner material, if valid deductions as to the uranium content of the bone as a whole are to be drawn from the analysis of a single powdered sample.

The results are of value in the following respect: The radioactivity of the Piltdown fossils could have been due either to uranium or to potassium of isotopic mass 40, and it can be shown that 1% of $K_2O$ is equal in $\beta$ particle activity to 0·0007% = 7 p.p.m. of uranium. The results obtained are accurate enough to show that the radiometric assays of Bowie & Davidson give a reliable figure for the uranium content of the samples examined, though difficulties in sampling, arising from differences in uranium adsorption with different bone or tooth structures, necessitate very careful interpretation of the results if the correct proportion of uranium in the bone as a whole is to be estimated.

TABLE XII.—*Uranium content of Piltdown and other fossils.*

| Reg. No. | Description | % $U_3O_8$ | $U_3O_8$ p.p.m. |
|---|---|---|---|
| E.590 | Piltdown I, left parietal | 0·0004 | 4 |
| E.591 | ,, I, left temporal | 0·0004 | 4 |
| E.592 | ,, I, right parietal | 0·0002 | 2 |
| E.593 | ,, I, occipital | 0·0008 | 8 |
| E.594 | ,, mandible | <0·00002 | <0·2 |
| E.596 | ,, *Elephas* cf. *planifrons* molar | 0·1 | 1000 |
| E.597 | ,, *Elephas* cf. *planifrons* molar, cementum | 0·1 | 1000 |
| E.620 | ,, *Elephas* cf. *planifrons* molar, cementum | 0·1 | 1000 |
| E.622 | ,, *Mastodon* molar | 0·002 | 20 |
| M.15709 | Swanscombe skull, occipital | 0·003 | 30 |
| M.17034 | Ichkeul "*Elephas* cf. *planifrons*" molar, dentine | 0·02 | 200 |

I acknowledge, with much pleasure, the loan of a fluorimeter by the Atomic Energy Research Establishment, Harwell, and the help given by Mr. R. A. Wells of the Chemical Research Laboratory.

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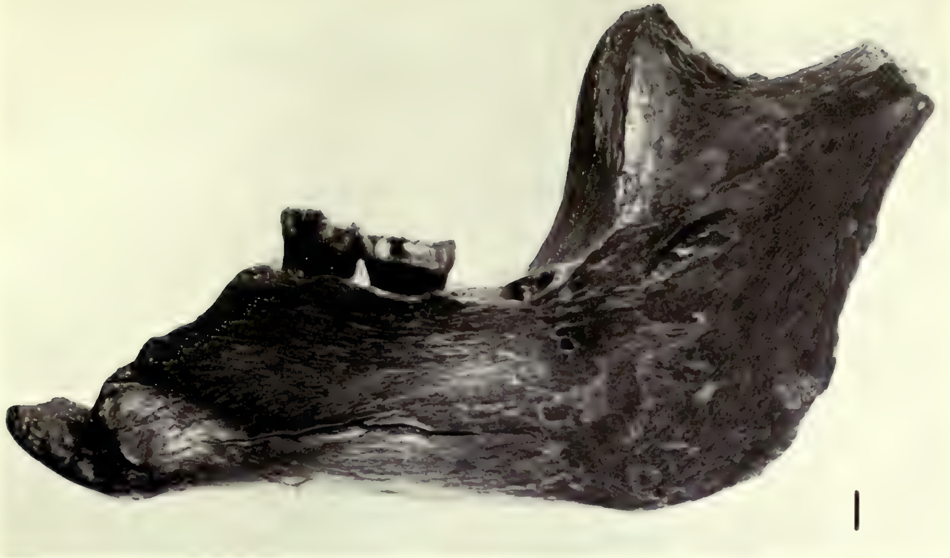
## EXPLANATION OF PLATES

### PLATE 27

Photograph of the medial aspect of (Fig. 1) the Piltdown mandible compared with (Fig. 2) a female orang mandible (unstained) which has been broken in the same manner as the " fossil " specimen, and in which the first and second molar teeth have been planed down to a corresponding level of dentine exposure. It should be noted that in the Piltdown mandible the angle has been slightly reduced by abrasion, and the lower margin of the mandibular foramen has been broken.

[*Photographs:* Fig. 1 by *C. Horton,* Fig. 2 by *F. Blackwell.*]



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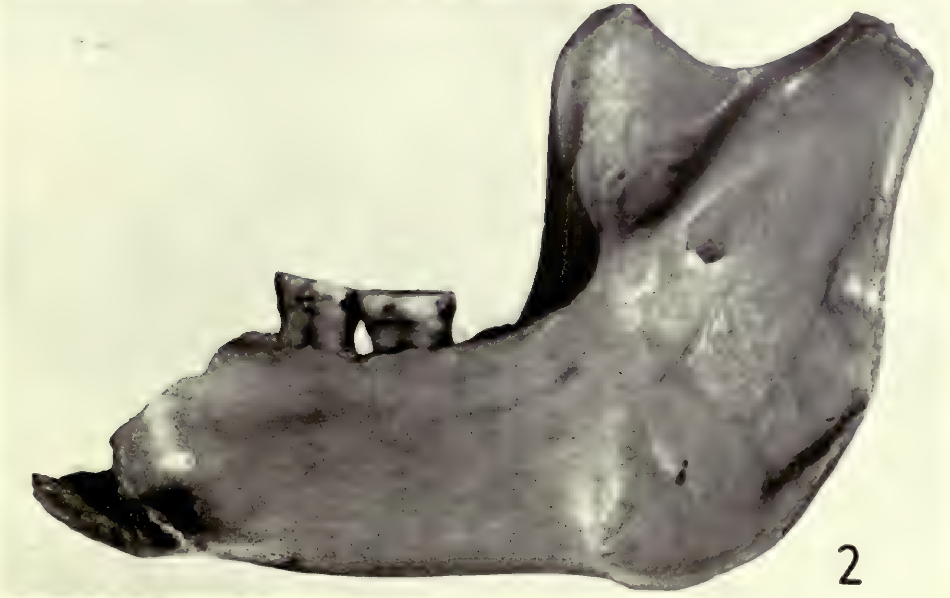

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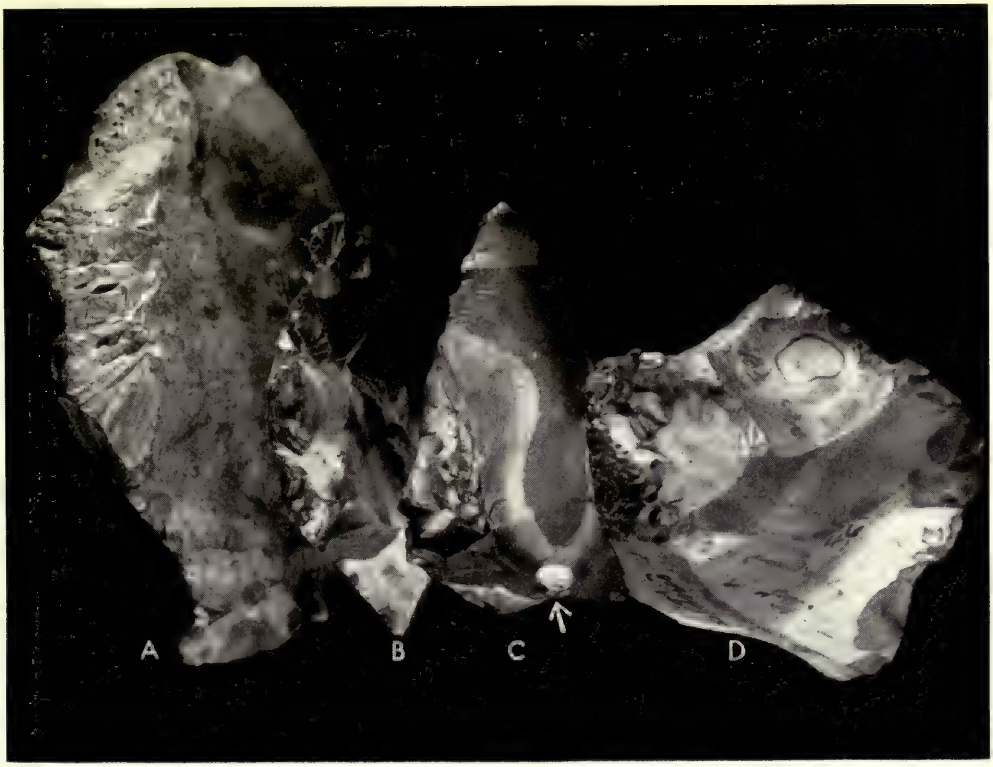
## PLATE 28

FIG. 3. (A–C) " Palaeolithic flint implements " recorded from the Piltdown gravel (left to right E.607, 605, 606) and (D) " Morris's " flint core (E.2690), all showing areas of intense localised battering. Note that where a chip (arrow) has been removed from E.606 the cortex is pure white below the superficial stain. × 2/3.

FIG. 4. The iron-stained surface of flint E.607 (A above). The speckly character of the stain is typical of artificial pigmentation of patinated flint. × 2.

FIGS. 5–6. Flaked surface of flint E.607 (Fig. 5) compared with the naturally iron-stained surface of a flint (E.965) from the Piltdown gravel (Fig. 6). The ink circles indicate areas which were wiped immediately after dilute hydrochloric acid had been applied to them. The stain on E.607 was removed, the natural stain on E.965 was unaffected. Natural size.

[*Photographs : C. Horton.*]



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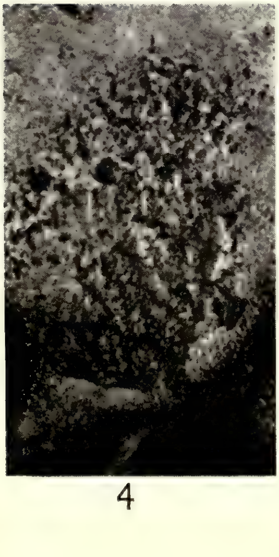

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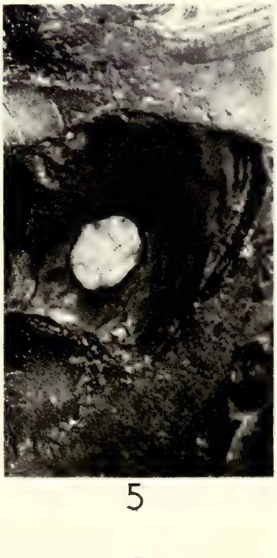

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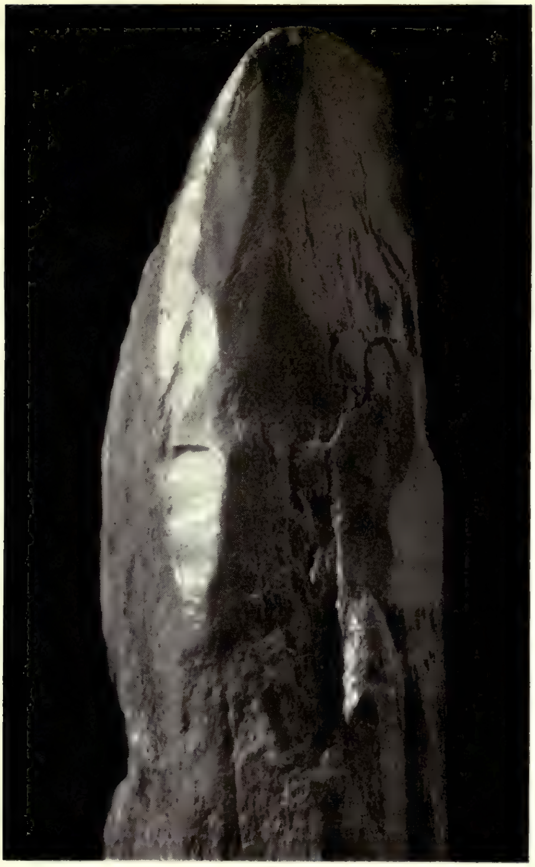
## PLATE 29

Figs. 7, 8. The pointed end of the Piltdown bone " implement ", showing details of the cuts on the lateral faces. E.615. Natural size.

Fig. 9. The cut facets at the rounded butt end of the " implement ". Natural size.

Fig. 10. A piece of fossil bone from the Swanscombe gravels which has been shaped with a steel razor and artificially iron-stained ; it reproduces all the essential features of the Piltdown bone " implement ". E.2707. × 2/3.

[*Photographs : C. Horton*].



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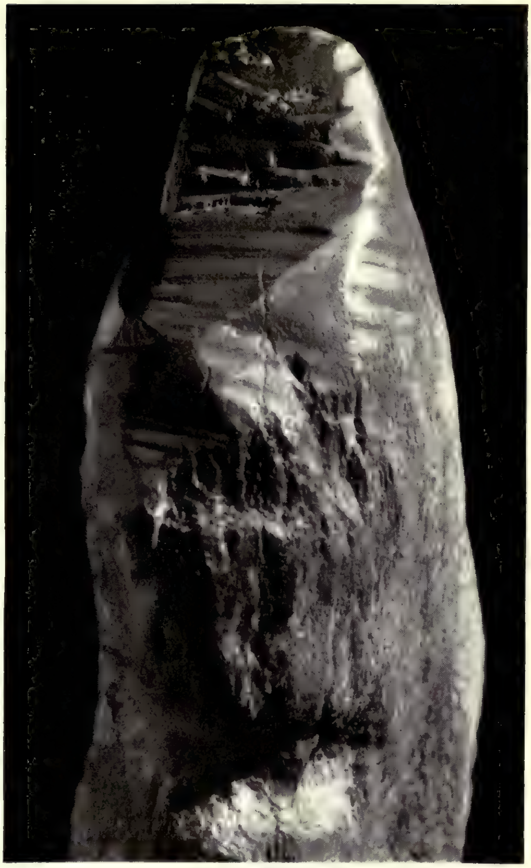

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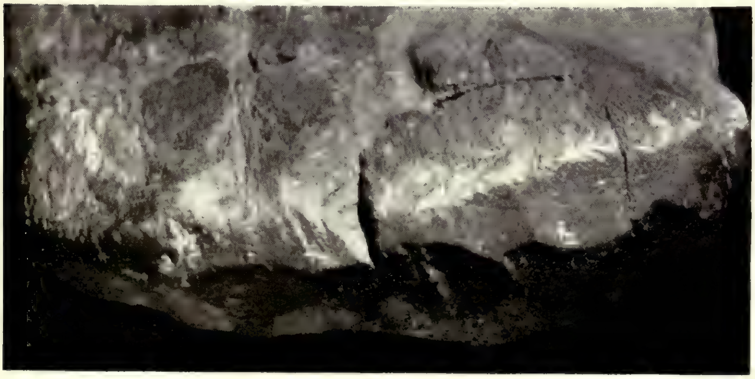

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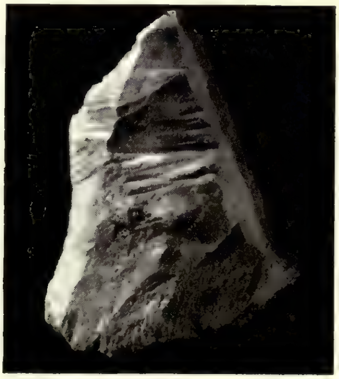

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## PLATE 30

FIG. 11. Electron-micrograph of decalcified residue of a sample of the Piltdown mandible, showing banded collagen fibres. × 30,000 (approx.)

FIG. 12. Section of fragment of molar tooth of *Elephas* cf. *planifrons* in the Piltdown collection (E.620). × 2.

FIG. 13. Autoradiograph (intensified) of the same section, produced by six weeks contact with very sensitive film (Ilford nuclear research pl., emulsion type B.2); demonstrating the high radioactivity of the dentine and cementum layers. × 2.

[*Photographs:* Fig. 11 by *A. V. W. Martin*, Fig. 12 by *C. Horton*, Fig. 13 by *S. H. U. Bowie.*]

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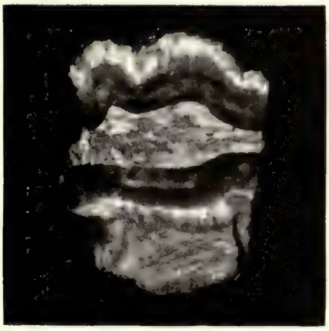

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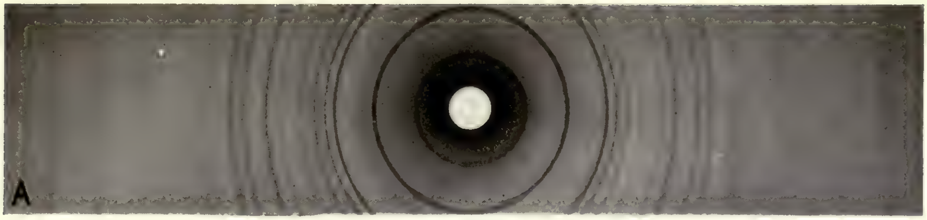
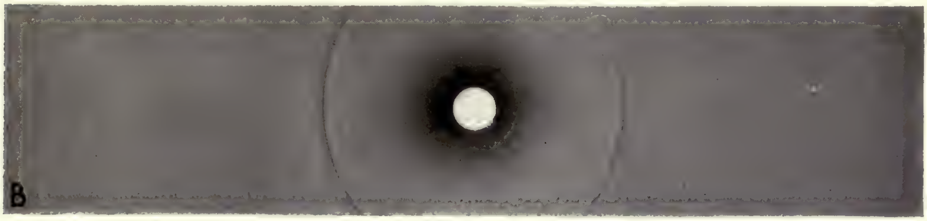
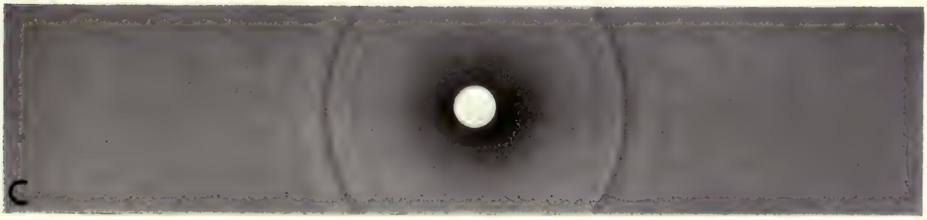
PLATE 31

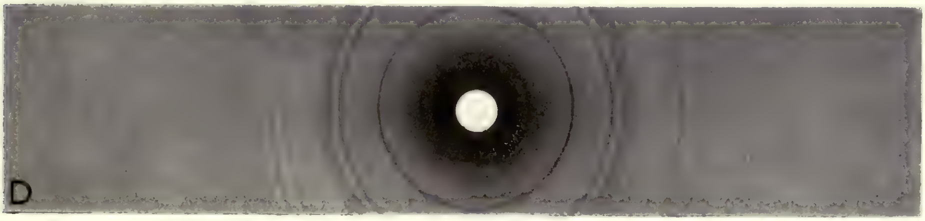
X-ray diffraction photographs on 6 cm. diameter camera ; Co-K$\alpha$ radiation. A. Gypsum (Mosul marble). B. Apatite (Jumilla, Spain). C. Apatite (Fragment of bone). D. Gypsum + apatite (Piltdown skull, frontal). E. Gypsum (Neolithic skull bone from Coldrum, Kent, soaked for 96 hours in 10% solution of iron alum).

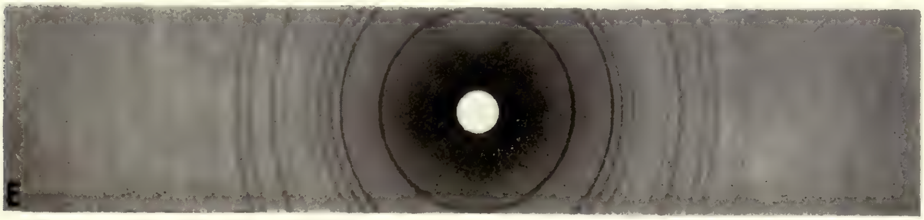
[*Photographs taken in the Department of Minerals.*]











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# THE SCHIZAEACEAE OF THE SOUTH OF ENGLAND IN EARLY TERTIARY TIMES

M. E. J. CHANDLER

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# THE SCHIZAEACEAE OF THE SOUTH OF ENGLAND IN EARLY TERTIARY TIMES

BY

MARJORIE E. J. CHANDLER

*Pp.* 291–314 ; *Pls.* 32–38 ; 2 *Text-figures*

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# THE SCHIZAEACEAE OF THE SOUTH OF ENGLAND IN EARLY TERTIARY TIMES

*By* M. E. J. CHANDLER

## SYNOPSIS

The paper records the discovery of two new species of *Anemia, A. poolensis* and *A. colwellensis*, and one of *Lygodium, L. poolensis*, in the early Tertiary strata of Britain. It also gives new information about *Lygodium kaulfussi* Heer from fertile material. Fertile pinnules of all these species are so beautifully preserved that more is now known in detail of some of these fossils than of many living species. Previous knowledge of British Tertiary Schizaeaceae is summarized. Fuller and more satisfactory evidence that the two genera once grew in southern England supports other evidence from fruits and seeds (awaiting publication) of a very warm and humid climate in the south of England throughout the early Tertiary period.

## INTRODUCTION

Previous knowledge of the Schizaeaceae in the English Tertiary was based on sterile fronds of *Anemia subcretacea* (Sap.), *Lygodium prestwichii* Gard. & Ett. and *Lygodium kaulfussi* Hr. together with some imperfectly studied fertile fragments of the last species. Like the contemporary angiosperms these ferns indicate a very warm and humid climate. They are perhaps survivors of an ancient widespread more or less uniform broad Mesozoic tropical belt of vegetation. For *Anemia* appears to be a relict genus in the old world, where it is now represented by few species although the genus was formerly widespread. But it flourishes and is represented by numerous species in the tropics and subtropics of the New World, albeit with a restricted northern range. *Lygodium* still holds its own in both hemispheres with a shrunken latitudinal area of distribution which can be attributed to the universal post-Eocene cooling of climate and consequent contraction of the tropical and subtropical belt of vegetation.

This paper is a bye-product of research upon the fruits and seeds of Tertiary Beds in Dorset, Hampshire, and the Isle of Wight. The material first to be described was found in abundance while sifting carbonaceous sands in the Lower Bagshot Beds (Cuisian ?) on the north shores of Poole Harbour at Lake, near Hamworthy, Dorset. The matrix was coarse and rich in seams of wood and fruits among which were small, often crushed and contorted, ovoid or subglobular, segmented bodies. The majority had tightly enrolled segments of distinctive appearance. When moistened with alcohol or nitric acid on a glass slide and examined under the microscope, quantities of large globular-tetrahedral spores were released among which were many larger turgid bolster-shaped or fusiform objects of spore-like appearance.

Further investigation showed that on the inner surface of the enrolled segments sporangia were seated apparently in two rows. They had the typical apical annulus of Schizaeaceae, but the occurrence of what appeared to be two types of spore presented a problem for which botanists who were consulted could produce no ready solution.

In due course the specimens were shown to the late W. N. Croft. With characteristic generosity and interest he gave up many hours to the investigation of the matter, studying with painstaking thoroughness not only the evidence yielded by the fossils, but all that could be discovered from living material of *Anemia*. In addition he searched the literature of Recent ferns, and such published work as is available on fossil Schizaeaceae in the hope of obtaining a clue to the mystery of the two types of " spore". As the result of a very large amount of work Mr. Croft discovered that the turgid elongate "spores" were really paraphyses such as are found growing among the sporangia on the surface of Recent fertile *Anemia* pinnules. The relationship of the fossils to *Anemia* was then demonstrated by cell-structure, sporangia and spore-characters and a spore-count. Mr. Croft was also responsible for most of the fine series of highly magnified photographs of sporangia, spores and paraphyses shown in the accompanying plates.

It was our original intention to produce a joint paper on this species, here named *A. poolensis*. But unfortunately Mr. Croft died before the work was finished. It therefore remains for me to record the results of our efforts and to pay tribute to the work of a most generous and able colleague. It can be claimed that more is known of the fruiting organs of the fossil species *A. poolensis* than of many of the living species of this large tropical and subtropical genus. The same species was found represented by one pinnule in somewhat younger beds at Sandbanks and at Branksome Dene in the Bournemouth Freshwater Beds (Lutetian ?) where several macerated pinnules occurred. It was represented at Cliff End near Mudeford (Auversian ?) by a minute fragment which yielded spores, and by a solitary spore at Alum Bay, Isle of Wight (Lower Bagshot, just above the pipe clay) where, according to Gardner & Ettingshausen (1880 : 47), Heer was confident he had seen a barren pinnule of *A. subcretacea*.

While working on *A. poolensis*, I had the good fortune to discover a tiny fertile pinnule of a second species of *Anemia* in the Upper Headon Beds of Colwell Bay, Isle of Wight. It is here described as *A. colwellensis*. In spite of prolonged search and sifting no second specimen has yet been found. It occurred in a small pocket of broken and battered fragments which included scraps of *Gleichenia*.

A second genus of Schizaeaceae, *Lygodium*, represented by fruiting pinnules of two species also turned up at about the same time. One was closely associated with barren pinnules of *L. kaulfussi* at Studland (Cuisian ?) and may be presumed to belong to that species. It was also found in the Bournemouth Freshwater Beds at Branksome Dene, Dorset. The species formerly occurred in considerable abundance at Bournemouth, chiefly as barren pinnules but rarely as fertile ones. The other was represented by a naturally macerated fertile pinnule in fine sediment at the base of the section at Lake. Its spores demonstrated beyond question that it is specifically distinct from *L. kaulfussi*. It has been named *Lygodium poolensis*. A solitary spore was subsequently recognized entrapped among the hairs of *Anemia* on slide V.31511.

The importance of these discoveries lies in the fact that hitherto the occurrence of Schizaeaceae in the south of England has been based on barren pinnules only, if we except the imperfectly investigated fertile tufts of *Lygodium* figured by Gardner & Ettingshausen from Bournemouth (see below). The fertile fragments hereafter described confirm the earlier work by providing fuller and more satisfactory evidence that the genera *Anemia* and *Lygodium* once grew in southern England. The presence of this essentially tropical family supports evidence from fruits and seeds (awaiting publication) of a very warm and humid climate in the south of England throughout the earlier Tertiary period.

Previous work takes account of three species only : *Anemia subcretacea* (Saporta) from the Bournemouth Freshwater Beds and Reading Beds, *Lygodium prestwichii* Gard. & Ett. from the Woolwich and Reading Beds, and *Lygodium kaulfussi* Heer from the Bournemouth and Studland Beds. A brief account of these three species as recorded in literature is given here, while *L. prestwichii* is also described from a new site at Newington, Kent and *L. kaulfussi* from fresh barren material from Studland as well as from the newly discovered fertile material. A few barren pinnules from the Bembridge Beds originally described as *Filix incertae sedis*, sp. 5, can now be referred with reasonable certainty to a species of *Anemia* although few of its characters are known. Its nervation and pinnule margins are strongly reminiscent of the fertile pinnule segments of *A. colwellensis*. As there is no definite connecting link between the two, however, the Bembridge pinnules must be regarded, for the time being at least, as representing a third species.

## Genus ***ANEMIA*** Swartz

NOTE : The spelling of the generic name is that given in the code of Botanical Nomenclature 1952, p. 83.

### ***Anemia subcretacea*** (Saporta)

1868. *Asplenium subcretaceum* Saporta, p. 315, pl. 23, fig. 4.
1880. *Anemia subcretacea* (Saporta) Gardner & Ettingshausen, p. 45, pls. 8, 9.
1882. *Anemia subcretacea* (Saporta) : Gardner & Ettinghausen, p. 67.
1886. *Anemia subcretacea* (Saporta) : Gardner, pp. 400, 402, pl. 1.

The fern is illustrated and fully described by Gardner & Ettingshausen (1880) from the Bournemouth Freshwater Beds, and is illustrated by Gardner (1886), but without full description, from the Reading Beds of Reading.

The specimens are preserved in the British Museum (Natural History) Geology Dept., Nos. V.14970–73 and V.15033–42 (Bournemouth) and V.15272 (Reading).

According to Gardner the barren pinnules were very abundant at Bournemouth especially to the east of Bournemouth pier, decreasing in size and abundance westwards towards Poole Harbour, while at Branksea only small pinnules occurred. He comments that the fertile pinnules, which he had never seen, were almost certainly separate and therefore rarely if ever preserved. He added that although the fern "did not agree very closely with any existing species of *Anemia*, the general form and dichotomy of the frond, the venation, the length and strength of the stipes, the separation of the fertile and barren pinnae, have, after much consideration, induced us to place it in the genus *Anemia*". He compared it with *A. adiantifolia* Sw. from Cuba, the Bahamas, Florida and Mexico to Bahia.

Gardner & Ettingshausen (1880 : 47) report that Saporta, who had evidently compared Bournemouth specimens with similar ferns from Sézanne, had no hesitation in stating that the two were identical, while Lesquereux compared them with some from the Eocene of North America and could see no difference whatsoever. Gardner & Ettingshausen (1882 : 67) add that the species is characteristic of the "older Eocene, and even pre-Eocene Rocks". They state that it first appeared in the Cretaceous and its upper limit in Europe is the Bournemouth horizon and that it attained its greatest luxuriance in the Eocene Beds of what are now temperate latitudes although it ranged from the south of France to the Arctic regions.

This barren foliage closely resembles specimens of *Anemia fremonti* Knowlton and *Anemia* sp. figured by Andrews & Pearsall (1941, pl. 5, figs. 30–32, 34, 35) from the Upper Cretaceous Frontier Formation of south-western Wyoming, U.S.A.

The discovery of abundant fertile pinnules of *Anemia*, described below as *A. poolensis*, in the Bournemouth Beds (Cuisian or Lutetian ?) of the western end of the Bournemouth section raises the question whether these detached fragments are the fertile form of *A. subcretacea*. The relationship cannot be proved in the absence of any organic connection and in the absence of the two forms in close association in the same layers. They are separated therefore for the time being although it is quite possible that future evidence may make it necessary to unite them under one specific name. Should this eventually happen the character of the spores (p. 301, Pl. 33, figs. 24–31 ; Pl. 36, figs. 54–58) would clearly separate *A. subcretacea* from *A. fremonti* forma *fertilis* Andrews and therefore presumably from the barren *A. fremonti* Knowlton. Nevertheless it is interesting that species of *Anemia* with the same type of foliage existed in Cretaceous and Eocene times in the two hemispheres, and that in both the genus extended far to the north of its main present day range in tropical and subtropical latitudes. In America *Anemia* is found only as far north as the Sierra Nevada and Florida but is richly represented by many species in Central and South America and the West Indies, especially in mountainous regions. In the Old World today it survives only as a relict genus with a very few species, one *A. lanipes* Christensen in Madagascar, one *A. schimperiana* Presl. in tropical Africa and South India, and one *A. dregeana* Kze in Natal. The genus may perhaps be regarded as a representative of that ancient more or less uniform tropical plant belt of low latitudes in Cretaceous times. For unknown reasons it persists as a vigorous component of the tropical and subtropical flora of the New World up to the present, but in spite of its former wide range in the old world it remains there now only in an attenuated form although in the equatorial belt the climate was probably always favourable to it. But outside the tropics where colder conditions prevailed after the Eocene it was exterminated altogether.

### *Anemia poolensis* n. sp.

(Pl. 32, figs. 1–10; Pl. 33, figs. 14–22, 24–31; Pl. 34; Pl. 35, fig. 41; P.l 36, figs. 54–58; Text-figs. 1, 2)

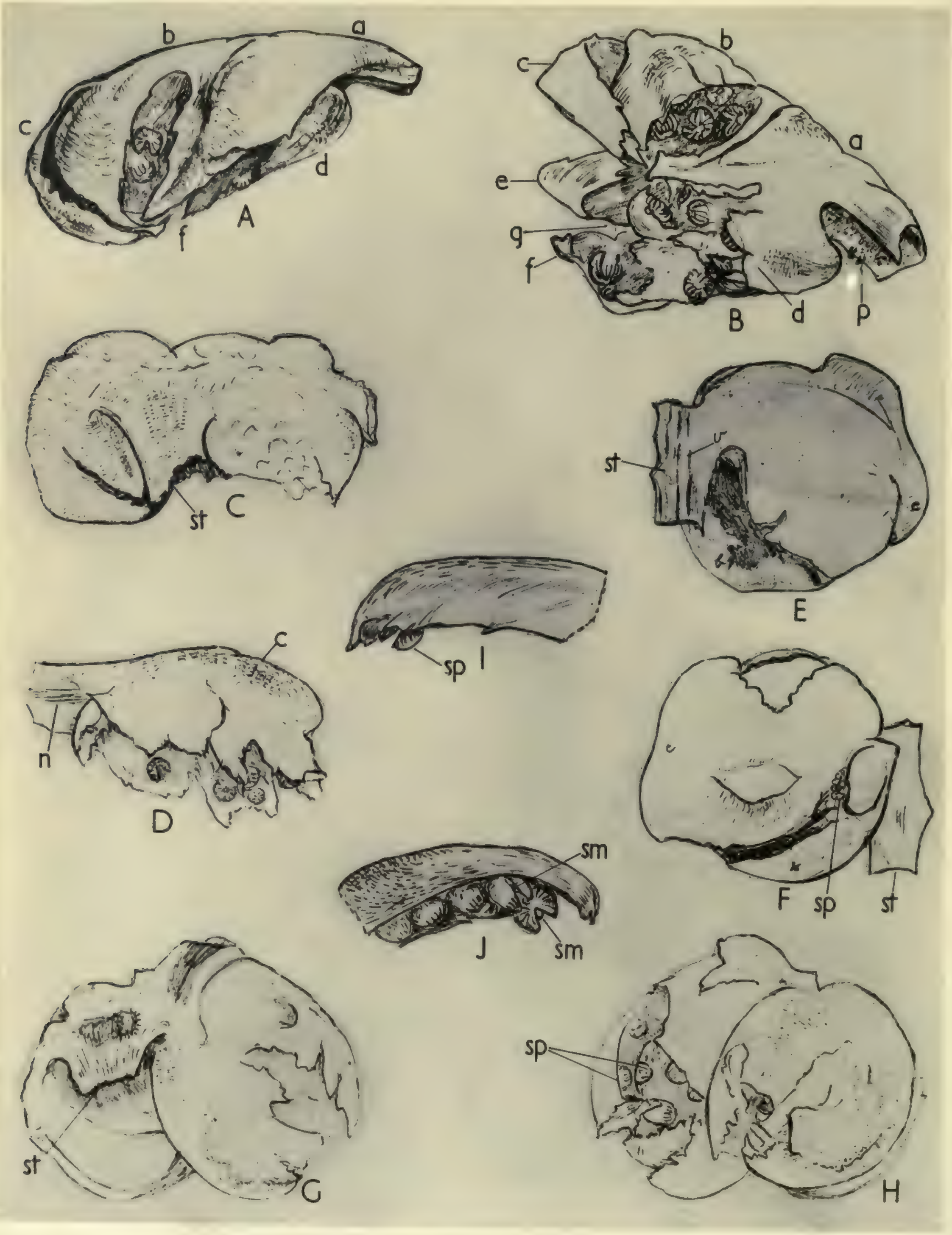
Diagnosis. Fertile pinnules deeply divided into a varying number of segments, 4 to ? 7, some of the segments being further dissected and often somewhat twisted. Segments strongly recurved so as to form a compact body about 2 or 3 mm. across (often open below), foliose, irregularly and deeply toothed or jagged especially distally, often sharply pointed, sometimes boat-shaped, occasionally clothed with a felt of pointed usually non-septate hairs which may occur on both surfaces. Sporangia numerous, sub-ovoid to sub-globular, about 0·25 to 0·44 mm. long and 0·2 to 0·3 mm. broad. Annulus symmetrical, apical, occupying about two-fifths of the length of the sporangium, formed of a single row of about fifteen straight thick-walled cells. Cells of sporangium wall almost straight superficially but when examined with ¼ in. objective having a finely sinuous appearance. Apical plate delicate of about 12–14 cells. Trilete tetrahedral-globose spores entirely smooth, about 50 to 60μ (rarely larger or smaller) in diameter, wall 2 to 2·5μ thick as seen in optical section. Paraphyses many among the sporangia, sessile or shortly stalked, about 72 to 156μ long, 48 to 114μ broad.

Holotype. V.31484.

Description. *Rhizome and frond* including fertile stipe unknown. Fertile spike probably somewhat flattened in one plane, by inference (see below).

*Fertile tertiary pinnae* having several segmented pinnules of which one is terminal while the others may spring from one stipe and form a pair of sub-globular bodies (Text-figs. 1 C, G, H) or they may arise singly (Text-figs. 1E, F; 2B).

*Fertile pinnules* divided sympodially into from 4 to at least 7 segments, some of which may be further dissected and much twisted. Segments strongly recurved so as to form a compact sub-ovoid, sub-globular, or ellipsoid "body" about 2 to 3 mm. across but varying in size with the degree of folding and recurving, largest in the least recurved specimens. Terminal pinnules more simply reflexed than the others in the few such specimens seen, and not enrolled at the distal ends of the segments so that the sporangia on their lower surfaces are partially exposed (Text-figs. 1A, B, D; 2G, H), other pinnules are usually open below to a lesser extent, for not all segments are enrolled distally, so that the "bodies" may gape downwards (Text-figs. 1H; 2A, E, F). Segments rather rigid, foliose, of variable width without indusium-like margins, irregularly and sometimes deeply toothed with sharply pointed narrow teeth and free tips. Hence their distal ends have a jagged appearance (Text-figs. 1A, B, G, H; 2D). These tertiary pinnules ("bodies") are often somewhat flattened. This appears to have been an original character as indicated by the form of the segments, those which form their lateral margins being frequently folded longitudinally and more or less inverted boat-shaped so that they embrace the adjacent segments (Text-figs. 1 I, J). Those over the middle part of the bodies may be broad or unfolded, they may even be slightly concave outwards with outward curving edges. The boat-shaped lateral segments are unequal sided as a rule, one side of the "boat" being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TEXT-FIGURE 1

## TEXT-FIG. 1. *Anemia poolensis* n. sp.

(A) Side view of a terminal pinnule from a fertile tertiary pinna. Stipe to right. Five recurved toothed segments (*a, b, c, d, f,*) are shown with a few sporangia exposed in the gaps between them. Direction of cell-structure indicated on the upper surface of the segment. Length, 3·1 mm. × 20 approx. Holotype V.31484.

(B) Under surface of the same. More of the recurved segments are seen *a, b, c, d, f,* as in A, *e, g,* additional segments not visible in A. Note the sporangia. Paraphyses were attached at *p*. × 20 approx.

(C) A pair of tightly reflexed downwardly directed pinnules (1) and (2) showing the broken end of the stipe (*st*) from which they spring. Length, 2·4 mm.; breadth across the pair, 3·25 mm. Surface much sand-pitted in places. × 17 approx. V.31485.

(D) A terminal loosely recurved pinnule. It was originally united on the left to a stipe which bore two other fertile pinnules (now detached). Length about 2·5 mm. ; height, 1·6 mm. (*n*) is a nervule flanked by fragments of reduced fronds. (*c*) Indicates shining cells with digitate walls. Under the microscope the walls appear raised and rounded, the centre of the cells depressed. There are sporangia on the lower surface. × 17 approx. V.31486.

(E) A tightly recurved and enrolled single pinnule still attached to a large fragment (1·4 mm. long) of stipe (*st*) of the tertiary pinna. The midrib of the stipe is channelled on the upper surface at (*v*), the channel marking a vein flanked by reduced lamina. (*b*) and (*c*) are two segments. Maximum diameter at right angles to stipe about 2·75 mm. × 15 approx. V. 31487.

(F) Reverse side of E. (*st*) stipe, (*b, c*) correspond to segments so labelled in E. A mass of spores liberated from a disrupted sporangium is indicated on the right at (*sp*).

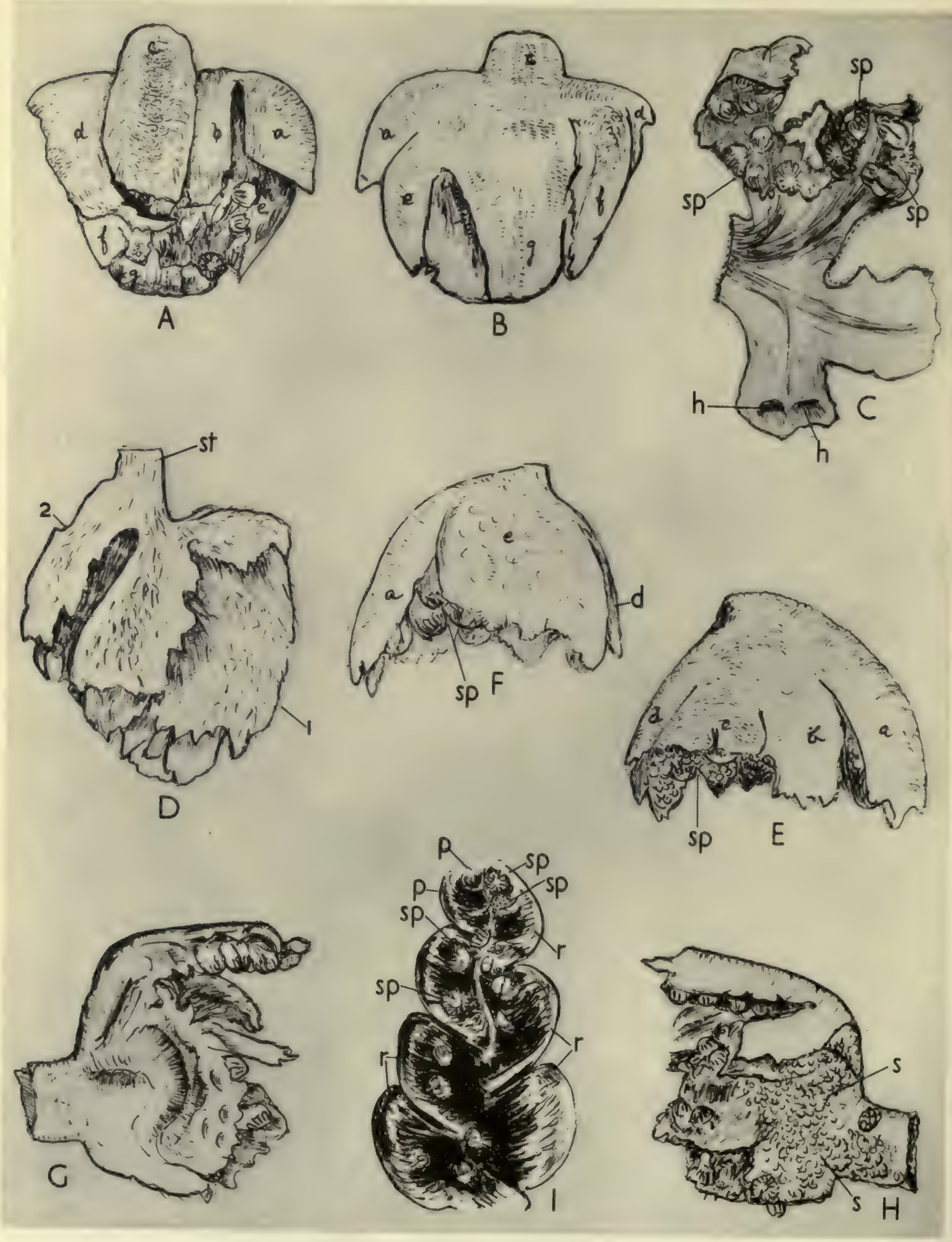
(G) A pair of tightly reflexed downwardly directed pinnules still attached to the remains of a stipe (*st*). Length about 2·75 mm.; across the pair, 3 mm. × 17 approx. V.31488.

(H) Reverse side of the same specimen showing the reflexed segments of the two pinnules, with a few sporangia (*sp*) exposed.

(I) A detached typical unequal-sided boat-shaped segment showing the upper surface. A sporangia projects from below at (*sp*) with open stomium. Oblique striae diverge from the nervule over the surface on this side of the segment. Proximal end to right. Length preserved 1·8 mm.; depth, 0·75 mm. × 20 approx. V.31489.

(J) Opposite side of the same segment which displays more of the under surface owing to the inequality of the sides of the segment. Proximal end to left. Six sporangia are shown, the two at the distal end with gaping stomium (*sm*) directed to the margins of the segment. Orientation of cells indicated on the upper surface. × 20 approx.

All the above are from Lake, nr. Hamworthy, Dorset.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TEXT-FIGURE 2

TEXT-FIG. 2. A–H. *Anemia poolensis* n. sp. I. *Anemia colwellensis* n. sp.

(A) Sharply reflexed pinnule with downwardly directed segments (*a–f*). A few sporangia are exposed where they gape. The direction of the cells, transverse over the middle of the segments, diverging near the edges, is indicated. Length, 2·25 mm.; breadth, 2·5 mm. (*g*) is the lower surface of the stipe. × 20 approx. V.31490.

(B) The reverse of A. Segments and stipe lettered to correspond with A.

(C) Part of an unrolled pinnule, lower surface. Tips of segments at the base of the figure appear to be broken.. The segments above retain their sporangia (*sp*). The segment below shows hollows (*h*) from which sporangia have fallen. The nervules of the segments are indicated where they could be traced. Maximum diameter of the specimen, 2·5 mm. Maximum length preserved measured along the nervule, about 1·5 mm. ×27 approx. V.31491.

(D) A pair of pinnules, one large (1) the other small (2) borne on the stipe (*st*). Segments much folded together. Surface covered with a felt of hairs, indicated only, in the drawing. Length, 3 mm.; breadth, 2·75 mm. This specimen yielded a smooth spore identical in all its characters with those of the smooth hairless specimens (see V.31506). × 17 approx. V.31492.

(E) A pinnule originally more or less complete but now with the tips of the segments broken. Segment lettered (*d*) may be the stipe. Direction of cells indicated on the surface. Sporangia and released spore masses are seen in the opening below. Length, 1·5 mm.; breadth, 1·75 mm. × 24 approx. V.31493.

(F) Opposite side of the above showing segments (*a*) and (*e*) much sand pitted. (*d*) again may be the stipe.

(G) Upper surface probably of a terminal pinnule. Sporangia are seen in profile in the segment at the top of the figure. The stomium opens outwards. Surface much sand pitted. Maximum length from tip of free segment to base of stipe (?), 2·5 mm.; breadth, 1·75 mm. × 24 approx. V. 31494.

(H) Opposite side of specimen showing the lower surface of the pinnule with a few folded and twisted segments. Sporangia are seen, but over most of this surface they have been disrupted so that the surface is concealed by a mass of released spores (*s*). × 24 approx.

(I) Lower surface of a fertile pinnule (the only specimen) which yielded all sporangia and spores figured (based on a drawing made before the specimen collapsed). It shows alternating, smooth-edged, rounded segments on opposite sides of the nerve or midrib, their recurved margins (*r*, *r*) which produce the smooth outlines form a fringe-like indusium covering part of the lobes on this surface. The sinuous midrib, and the pocket-like depressions (*p*, *p*) from which sporangia have fallen can be seen. The arrangement of sporangia (*sp*, *sp*) in the lobes on each side of the midrib is indicated. × 20 approx. Holotype. V.31522. Colwell Bay, Isle of Wight.

Figs. A–D, G, H are from Lake, Dorset. Figs. E, F from Sandbanks, Dorset.

considerably broader than the other (Text-figs. 1 I, J). The flattening of the tertiary pinnules suggests that the fertile spike had a tendency to be flattened in one plane in life, but the character seems not to have been constant.

Both surfaces are sometimes clothed with a close felt of red or black pointed usually single-celled hairs (Pl. 32, fig. 6 ; Text-fig. 2D) pitted or corroded in fossilization. In the majority of specimens seen, these have disappeared, if they were ever present, and a highly characteristic glistening outer (upper) surface is exposed. This is formed of transversely elongate cells over the median longitudinal part of each segment, the cells being also aligned in longitudinal rows. As seen by reflected light they are rather coarse with sinuous outlines having sunk centres and raised margins so that they produce a conspicuous and highly characteristic pattern. In section (Pl. 34, figs. 32, 34, 37) more than one layer of these cells is seen and they appear thin-walled. Towards the edges of the segments the coarse cells give place to finer narrow elongate ones which form oblique striae diverging from the median band of shining cells. Inner or lower surface of the pinnule with similar narrow cells which diverge obliquely from the median line or venule of each segment towards its margins. Venules with ? scalariform thickening (Pl. 34, fig. 36). Granules like chloroplasts are common in many of the cells and also amongst macerated spores. They may occur singly or in groups (Pl. 32, fig. 10; Pl. 34, figs. 37, 38; Pl. 35, fig. 41) and appear sometimes to be aggregated into small irregularly shaped plates in which the boundaries between the grains are more or less obscure. The grains are usually rounded or oval but sometimes subangular. Their average size is about 2·5 to 3·5$\mu$. Similar granules occur in living *Anemia*, e.g. in *A. phyllitides* (L.) where they are greenish and about 3·5$\mu$ in diameter but they may be as large as 6$\mu$. In form and occurrence they are like those of the fossil.

*Paraphyses* (inflated short sterile filaments) (Pl. 33, figs. 18–22 ; Pl. 34, fig. 37) are abundant all over the lower surface of the pinnules growing amongst the sporangia. They are sub-ovoid to ellipsoid, usually straight, rarely slightly curved, sometimes with a fairly prominent point at the distal end, and a very short stalk at the proximal end. Sometimes they are asymmetrically attached. A few may be sessile. When freshly released from the pinnule segments and scarcely macerated they are shining and turgid, and dark brown in colour. On maceration they quickly collapse, the brown layer within cracks and tends to disintegrate revealing that the paraphysis wall is extremely thin in optical section. The size varies from about 72 by 48$\mu$ to 156 by 78$\mu$ or they may be as broad and short as 114 by 114$\mu$.

The *Sporangia* (Pl. 32, figs. 4, 5, 7–10 ; Pl. 33, figs. 14–17 ; Pl. 34, figs. 33–35, 37 ; Pl. 35, fig. 41) are shortly stalked (? sometimes sessile) borne in two rows which are closely spaced, alternating and forwardly directed. They arise from the venule or from points close beside it (Pl. 32, fig. 4). In the inverted boat-shaped lateral pinnule segments they project conspicuously above the narrow side of the segment (Text-fig. 1J). They are sub-ovoid, rather broad at the base, attached asymmetrically (Pl. 32, figs. 7, 8). The annulus is apical, symmetrical, well-developed and conspicuous, consisting of a single row of about 15 straight-sided cells (excluding the stomium) the internal and radial walls being strongly thickened. Length of annulus about two-fifths of the length of the sporangium (Pl. 32, figs. 4, 5, 7–10 : Pl. 33, figs. 14–17). The stomium consists of two to three rows of cells, dehiscence is longitudinal extending the whole length of the sporangium, normally occurring on the face towards the outer side of the segments (Pl. 32, fig. 5; Pl. 33, figs. 14, 15; Text-fig. 1J). Apical plate small and circular, very delicate, its distal face with about 12–14 cells, those nearest the centre of the plate equiaxial, five or six-sided with straight sides, those near the edge of the plate broader in a tangential than in a radial direction (Pl. 33, figs. 15, 17). The cells of the sporangial wall appear straight superficially with a 1-in. or ½-in. lens, sometimes they are rounded, at other times pointed at their extremities, elongate parallel to the major axis of the sporangium. When seen from the interior or examined with a ¼-in. lens they show a bead-like thickening (Pl. 32, fig. 8) which produces the effect of fine sinuosities on the external surface. Spore output probably 128 (115 actually counted). Length of sporangium about 0·25 to 0·44 mm., breadth about 0·2 to 0·3 mm.

*Spores* (Pl. 33, figs. 24–31; Pl. 36, figs. 54–58) trilete, tetrahedral-globose, non-striate, smooth, glistening, normally about 50 to 60$\mu$ in diameter but occasionally as small as 36$\mu$ and as large as 70·4$\mu$; about 2 to 2·5 $\mu$ thick, splitting occasionally along the triradiate mark, the distal ends of which sometimes show a fine forking in unsplit specimens (Pl. 33, fig. 27; Pl. 36, fig. 54).

REMARKS. These curiously rolled fertile pinnules were chiefly found in the coarser carbonaceous seams at Lake. Numerous specimens have so far been collected and many more would reward persistent collecting and sifting. More than sixty are available for study by reflected light and will be catalogued in a forthcoming British Museum monograph. Many others have been macerated to varying degrees and mounted on slides for examination by transmitted light.

The arrangement of the segments was at first very difficult to discover, but once seen it could be detected almost invariably especially after microscopic examination. In order the better to show structures which are even more obscure in the photographs than in the specimens themselves, sketches have been made (Text-figs. 1 and 2) which are essential to the understanding of these confusing specimens.

The technique adopted in the study of the material was as follows: they were at first examined as a whole by reflected light, a method which best showed the form and alignment of the surface cells, and the arrangement of sporangia and paraphyses on the segments. Many specimens or segments of pinnules were then macerated in nitric acid and mounted, some in xylol, others in Euparal or Canada balsam. They were then examined by transmitted light, and in the case of the denser specimens by strong reflected light using a white background. In this way some of the most delicate structures were seen and photographed. The apical plates of the sporangia were most difficult to display as their delicate cells were peculiarly liable to collapse and tear on maceration. They were most easily seen when mounted in glycerine; when transferred to alcohol they were frequently disrupted.

Spores and paraphyses were readily released from the sporangia or pinnule segments on moistening with alcohol or nitric acid. The spores were tough and resistant but the paraphyses were so thin-walled that they frequently collapsed as described on p. 300.

A series of microtome sections were prepared under the direction of W. N. Croft.

His notes show that they were cut by Mr. S. Prudhoe from a specimen which was thereby destroyed ; it is now represented by slides V.31506–07, V.31509–10. The " body " was impregnated with paraffin wax after treatment with hydrofluoric acid by the method described by Lang (1929 : 667–8). A first series of microtome sections cut at 10$\mu$ (slide V.31507) produced rather incoherent sections and the specimen was re-embedded. A second series was cut at 6$\mu$ (slide V.31510). Although less incoherent it was re-embedded. A third series was cut at 10$\mu$ (slide V.31509). It held together fairly well but the centre came away as loose powder, due, it was thought to the toughness of some of the tissues. The remaining piece was softened by treatment with tribasic sodium. The fourth series (slide V.31506) was cut from the softened tissue but it appeared to be little better. It was spoilt by the cover-slip sliding over the sections during cleaning. Some of the sections are illustrated in Pl. 34, figs. 32–38.

Fertile pinnules of Recent *Anemia* vary considerably in habit. They may be scarcely foliose, or broad and leaf-like. They may have flat segments, or folded ones sometimes of boat-like appearance. The segments whether flat or folded may be reflexed and the whole pinnule rolled backwards like a tightly clenched fist, or they may be only slightly recurved or not reflexed at all. The species whose pinnules compare most closely with the fossils in general appearance appears to be the South American *A. gardneri* Hook., but in it the segments are fewer or more tightly enrolled, less rigid and less conspicuously jagged at the margins than in *A. poolensis* (Pl. 32, figs. 11–13). The species *A. schimperiana* Presl. from Angola also has closely folded pinnules in some herbarium material examined. A rare species from Madagascar *A. lanipes* Christensen is somewhat illuminating. Normally, its pinnules appear to be flattened in one plane and they are so described by Christensen. But a sheet No. 2798 (G. F. Scott Elliot Herbarium, Royal Gardens, Kew, 986) shows some pinnules definitely reflexed and rolled in varying degrees. In the most extreme instance the tightly rolled pinnules form sub-globular bodies 1·5 to 2 mm. in diameter. Perhaps this pinnule had become desiccated in life and had curled as the result, thereby protecting the sporangia on its lower surface. A similar tendency to protect by curling can be observed in British ferns growing in situations liable to periodic desiccation such as walls or crevices.

In *A. poolensis* the rolling of the pinnules appears to be a more or less constant character and it seems to be among terminal pinnules that rather flatter or less recurved specimens are found. Presumably the rolled up " bodies " were torn from the stipes by the battering they suffered from flood waters as they were swept to the places of deposition among angular quartz sand and coarse woody fragments.

*A. lanipes* is a peculiarly hairy species. *A. schimperiana* is also covered by a close felt of rather long hairs. The hairs of *A. schimperiana* are sparsely septate, long, swollen at the septa with a transverse diameter of 20 to 30$\mu$ across the cavity. Those of *A. lanipes* and *A. perrieriana* Chr. are similar so that they differ definitely from the fossil. Some Recent species have no hairs but are thickly beset with paraphyses like those of the fossil, e.g. *A. phyllitides* and *A. gardneri*. Some species, like the fossil, have both long hairs and turgid paraphyses, e.g. *A. schimperiana*. So far no non-septate hairs have been found in the few living species examined. Often the paraphyses in the living are less convex on one side than the other, or they may be concave on one side giving a curved form in profile. Others are symmetric. The basal end is not infrequently more rounded and blunter than the distal, and attachment is commonly by a short stalk either centrally placed or on one side. Paraphyses in *A. gardneri* were 110 × 55$\mu$ and in *A. phyllitides* 43 to 59$\mu$ long, 18·75 to 21·875$\mu$ broad. A paraphysis wall was measured in *A. schimperiana*. In optical section it was about 1–2$\mu$ thick.

The spores of the fossil, *A. poolensis*, appear to be unique in having a smooth glistening surface, but among the 115 living species of *Anemia* there are some whose spores are still unknown, and others which it has not been possible to examine. Nevertheless, many species were studied by Mr. Croft in the Herbarium of the Botanical Department of the British Museum (Natural History). The majority show highly characteristic ridged spores. The ridges may be smooth, tuberculate, or spiny. In some species the spore outline is more or less triangular, in others globose-tetrahedral. The size shows some little variation, e.g. 56 to 87·5$\mu$ in *A. gardneri* Hook. with a wall of about 4$\mu$ thick ; 75 to 100$\mu$ in *A. schimperiana* Presl. ; 93·75 to 106·25$\mu$ in *A. adiantifolium* Swz. ; 53 to 70·7$\mu$ in *A. perrieriana* Chr., wall 3 to 5·8$\mu$ thick ; about 81$\mu$ in *A. lanipes* Chr. Thus they tend on the whole to be larger than those of *A. poolensis* (50–60$\mu$) which corresponds in size more closely with those of the American species *A. fremonti* forma *fertilis* Andrews. These according to Andrews & Pearsall (1941 : 169) show a considerable range from 25 to 47$\mu$ with an average of about 40$\mu$ ; some measured by the writer were as much as 50 or 53$\mu$. The only smooth spores seen were immature examples of *A. perrieriana*. They had thick firm walls. One plant gave smooth spores only, but the next on the same sheet and no doubt from the same gathering had mature smooth-ridged spores. In this species, as Mr. Croft noted, the spores become thick-walled prior to the formation of ornament. The ridges vary in their distance apart in different species and also in their smoothness or degree of ornamentation as will be further discussed on p. 306.

Thus while the apical annulus indicates the family Schizaeaceae beyond doubt, the generic relationship calls for careful consideration. The reflexed enrolled fertile pinnules, annulus with a single row of cells, many-celled apical plate, and spore size, all point to *Anemia* as the nearest living genus, but the smooth unridged spores, differing from the mature spores of known species, are peculiar to the fossil and require some explanation. Can they possibly be regarded as immature spores like those of *A. perrieriana* described above ? or as mature spores, originally ridged but denuded in fossilization of an ornamental exine ? or should the fossils be separated on the grounds of smooth spores and non-septate hairs as a distinct genus ? While there can at present be no absolute proof of the generic status, the following considerations appear to the writer to justify the use of the name *Anemia* at least provisionally.

(1) The sporangia have constantly (although not invariably) dehisced naturally as if they were fully mature, but in undehisced specimens which have been protected by the sporangium wall the spores show the same smoothness.

(2) Smoothness of spore is an invariable feature in every pinnule examined and is seen not only in the Lake material but wherever the species has been found. It is

most improbable that only immature material would have been found in different localities and among so many different gatherings.

(3) Against the view that an ornamental exine has been lost in fossilization is the fact that a second species from Colwell (see p. 305) has typical ridged spores although this material has been far more macerated in fossilization than that now under consideration.

(4) In two fossil species of *Lygodium* hereafter described (pp. 308, 312), one has consistently smooth spores, the other has highly ornamental spores while the majority of living species of *Lygodium* have spores ornamented in various distinctive ways, though *L. elmeri*, for example, has smooth spores. It seems unreasonable, when smooth and ornamental spores can both occur within a related genus, to make smoothness a reason for separating *A. poolensis* generically from living *Anemia*. Possibly smoothness of spore is a primitive character which still persists in *Lygodium* to a small degree but is now lost in living *Anemia* so far as present knowledge goes. On the whole the balance of probability appears to the writer to justify reference of the fossil to the genus *Anemia* itself, although it must be admitted that the last word may yet remain to be said.

*Anemia* is an herbaceous genus. Some examples of habitat are here quoted from herbarium sheets at Kew: 1,500 metres in Angola, 3,000–4,000 ft. in Cuba, 1,500 ft. in Mexico, 3,900 ft. in New Granada, 5,000 ft. in Madras in the Nilghiri Hills. There are records of " shady rock crevices", "summit of dry mountain ranges", " wet rocks", " by the river ", " on rich moist shady banks under shrubs ", " moist calcareous river bluffs ", crevices in vertical side of limestone rock " and " rocky pine-woods ".

### *Anemia colwellensis* n. sp.

(Pl. 35, figs. 39, 40, 42–53 ; Pl. 36, figs. 59–64 ; Text-fig. 2, 1)

DIAGNOSIS. Fertile pinnule flat, about 2·5 mm. long, 1·7 mm. broad, with several (at least 8 ?) rounded alternating segments on opposite sides of a nerve. Free outer margins of segments sharply recurved on to the lower surface so as to give a smooth outline and to form a false fringed indusium. Main vein of pinnule sinuous. Nervation of segments flabellate, the nervules repeatedly forked and free. Upper surface smooth, without hairs ? Sporangia in two rows on the lower surface of each segment, sub-ovoid, somewhat laterally compressed giving a slight bisymmetry ; sessile, broadly attached by the whole breadth of the base. Length of sporangium very variable, maximum about 228 to 342$\mu$ ; breadth about 171$\mu$. Annulus slightly bisymmetric, apical, conspicuous, formed by a single row of about 15 cells with extremely thick walls, occupying about one-half to one-third of the length of the sporangium. Trilete tetrahedral-globose spores ornamented with ridges which give the effect of tubercles where seen in profile at the margins. Diameter of spores 37·5 to 66·6$\mu$, commonly 43 to 50$\mu$. Height of spores from back to front 37·5 and 43·75$\mu$ in two specimens measured. Distance between ridges about 3 to 6·25$\mu$. Paraphyses many among the sporangia, sessile or shortly stalked, about 114 to 120$\mu$ long, 48 to 72$\mu$ broad.

HOLOTYPE. V.31519–23.

DESCRIPTION. *Fertile pinnule* 2·5 mm. long, 1·7 mm. broad, having several (at least eight) short, rounded, closely contiguous segments situated alternately on the opposite sides of a nerve and inclined to it at angles of about 45° (Text-fig. 2, 1). The free outer margins of the segments are sharply recurved on to the lower surface thereby giving the peculiarly smooth, rounded outline shown and producing a flat false indusium on the lower surface, which partially covers the sporangia. The " indusium " is striate and marginally fringed, the alignment of the fringe being parallel with the planes of separation between the segments and corresponding with the cell-structure (Text-fig. 2, 1). Main vein of pinnule sunk in a sinuous channel on the upper surface, not actually seen on the lower where it was obscured by sporangia and masses of released spores. Nervation of segments flabellate, the venules being repeatedly forked and free as in the living *Anemia* and as in *Anemia* sp. 3 (see Pl. 36, fig. 65). Upper surface smooth and free from hairs, lower surface with turgid brown sub-fusiform paraphyses among the sporangia showing, when highly magnified, a curious transverse streaking perhaps due to stretching caused by crushing as it is not always apparent. The paraphyses may be shortly stalked but are usually rather broadly based. They are thin-walled and about 114 to 120$\mu$ long, 48 to 72$\mu$ broad (Pl. 35, figs. 47, 48). One fragment of pinnule segment showing the distal margin appeared to be at least two cells thick and displayed oblong, almost rectangular, cells about 6 to 12$\mu$ in diameter with very fine closely digitate (sinuous) walls. The free ends of the nervules in this fragment were about 12$\mu$ apart.

The sporangia (Pl. 35, figs. 39, 40, 42–46) are large although they vary considerably in size with the degree of development and possibly with their position on the pinnule. The largest are about 228 to 342$\mu$ long and about 171$\mu$ broad. They are sub-ovoid but somewhat flattened so as to be bisymmetric, sessile and broadly attached by the whole breadth of the base, tearing away from the surface of the pinnule in a ragged manner often with fragments of epidermis still adhering. The apical annulus is in some cases somewhat bisymmetric owing to the flattening, it is a conspicuous feature sometimes bulging out beyond the sporangial wall below, occupying from one-third to one-half the length of the sporangium. It consists of a single row of at least 15 long narrow cells with straight thick walls which fork conspicuously at their lower extremities where they alternate with the thinner cells of the sporangial wall. Dehiscence longitudinal with stomium long and conspicuous. Its cell-structure is obscure owing to the denseness of the material and its broken character. It appears to have been directed towards the margin of the segment when in the position of growth. Apical plate multicellular, delicate, of angular equiaxial cells. Cells of sporangial wall elongate parallel to the major axis of the sporangium (Pl. 35, fig. 45), about 24$\mu$ broad, straight superficially, unevenly thickened so as to have a " beaded " appearance when seen from the interior. They contain numerous rounded or angular bodies which may have been chloroplasts but they are now heavily pyritized and glistening (Pl. 35, figs. 42, 43, 45). Spores (Pl. 35, figs, 49, 53 ; Pl. 36, figs. 59–64) trilete, tetrahedral-globose, somewhat triangular in outline, conspicuously but finely ridged, the ridges when seen in profile giving a false tubercled appearance to the outline of the spores. Distance between the ridges varies in different parts of the spore and may be from 3 to 6·25$\mu$. The distal ends of the rays sometimes fork, and splitting may occur along the rays (Pl. 36, fig. 62). The diameter of the spores varies from 37·5 to 66·6$\mu$ and is commonly from 43 to 50$\mu$. The height from the dorsal to the ventral side is more or less equal to the diameter. Two measurements of height were 37·5 and 43·75$\mu$.

REMARKS. One fertile pinnule more or less complete. This minute fragment was so tender that it fell to pieces on attempting to lift it on to a slide. Fortunately a drawing of the under surface had been made and a preliminary examination of both surfaces. Even more fortunately it was possible to make several slides of the remains showing sporangia, annuli and spores. Paraphyses are also preserved on the slides, but there are no indications of a felt of hairs. A small fragment of the pinnule itself is mounted on one slide showing nerves and cell-structure. The slides are rather opaque as the material was too scarce to risk destroying it by more than a slight degree of maceration in nitric acid. The character of pinnule, sporangia and and spores indicates the genus *Anemia* without question. Fortunately, in this case, the spore ornamentation is typical of *Anemia*. It is significant that the ornamentation is preserved in spite of the rotten and fragile state of the pinnule fragment, so much more rotted in fossilization than the pinnules of *A. poolensis*. The flat unreflexed pinnule with fringed false indusium formed by the reflexed margins of the short smooth-edged segments, the short broadly attached sporangia without hint of narrowing or arising from a stalk, the large deep annulus and the ridged spores, distinguish this species without any doubt at all from *A. poolensis*. Study of some of the many living species of *Anemia* indicates that the ridges on the spores vary to some extent in different species in their distance from one another and in their ornamentation. Thus in *A. schimperiana* the ridges are simple, not tubercled, and the spores sharply triangular with clear translucent rounded projections at the angles. The ridges are about 6$\mu$ apart. In *A. gardneri* the ridges bear contiguous tubercles which are a conspicuous feature, the tubercles being about 6$\mu$ in diameter. In *A. adiantifolium* the spore has round translucent angular projections, the ridges are smooth, and about 10$\mu$ apart. In *A. lanipes* they are sharp and thin, and may be 6$\mu$ apart, although sometimes closer. *A. aurita* Sw. has ridges with tubercles, *A. anthriscifolia* Schrad. has smooth or minutely echinulate ridges. In *A. perrieriana* the surface of the spore is ridged coarsely. *A. affinis* Bak. has large spiny spores. The ridges on the fossil *A. fremonti* forma *fertilis* are about 2·1 to 2·5$\mu$ apart. *A. phyllitides* has spines or long pointed tubercles arranged on ridges in the mature spores. It would involve prolonged study to attempt any sort of classification of the genus by its spore characters or even to prove conclusively that such was possible. Such a study cannot be undertaken for the purposes of this paper but knowledge of *Anemia* is incomplete without it.

The pinnule segments of the fossil recall *A. imbricata* Sturm. (Brazil), *A. ferruginea* —a hairy species from Central America (= *A. fulva* Hook.), the flat pinnules of *A. lanipes* (Madagascar), and *A. tomentosa* Sw. (warm America from Mexico and the Antilles to Peru and the Argentine). More fossil material is needed to complete the record of this interesting fern. But whatever view may be taken of the generic position of *A. poolensis*. the presence of *Anemia* in Southern England is indisputably established by the tiny fertile fragment described above as *A. colwellensis*.

### *Anemia* sp. 3

(Pl. 36, fig. 65)

1926. *Filix incertae sedis*, sp. 5 ; Reid & Chandler, p. 39, pl. 1, figs. 10, 11.

To the description previously published may be added the additional fact that some of the pinnules are asymmetric. There can be little doubt that this fern belongs to *Anemia*. For details of pinnules and nervation see Reid & Chandler (1926). The characters of these barren pinnules closely resemble those of the pinnule segments of *A. colwellensis* both in the smoothness of their margins and in the flabellate nervation. It is interesting to speculate whether the Bembridge specimens can possibly be barren material of *A. colwellensis*, but there the matter must rest until further evidence is available to prove or disprove their specific identity.

## Genus ***LYGODIUM*** Swartz

### ***Lygodium prestwichii*** (Gardner & Ettingshausen)

(Pl. 36, figs. 66–69)

1854. *Asplenium* sp.? Prestwich, p. 156, pl. 3, fig. 6.
1880. *Pteris* (?) *prestwichii* Gardner & Ettingshausen, p. 53, pl. 10, fig. 8.
1886. *Lygodium prestwichii* (Gard. & Ett.) Gardner, pp. 400, 401, 403, pl. 2, figs. 2–4.

DIAGNOSIS. Pinnae simple, elongate lanceolate-linear or cleft. Veins diverging at a sharp angle from the midrib, crowded, forking once or twice, midrib considerably thinned towards the apex. Fertile pinnules borne around the toothed margins of the barren pinnules ? Sporangia, spores and fertile pinnules unknown.

NEOTYPE. V.24862.

REMARKS. Fragments of this fern were found at Counter Hill, Lewisham, by Prestwich (1854, pl. 3, fig. 6 ; see also Gardner & Ettingshausen 1880, pl. 10, fig. 8), and by Gardner at Croydon and Woolwich (Gardner 1886, pl. 2, figs. 2–4). Gardner considered all these specimens as identical specifically after comparing his own material with that of Prestwich (1886 : 403). He regarded the species with its sparsely-toothed pinnules as characteristic of the Woolwich Beds and as quite distinct from *Lygodium kaulfussi* from Bournemouth. One fragment figured by Gardner (1886, pl. 2, fig. 2) shows a " toothed " margin, the projections being (so he states) the bases of fertile segments removed in fossilization. Unfortunately the Prestwich pinnule from Lewisham seems to have disappeared (Gardner & Ettingshausen, 1880 : 53) and even Gardner's Woolwich and Croydon specimens cannot now be traced. It is therefore fortunate that a few fragmentary pinnules with toothed margins which apparently belong to the same species were collected more recently by the late H. C. Berdinner in beds at Newington. From the locality and their appearance they may be presumed to be of Woolwich age. They are impressions only representing fragmentary pinnules. One (V.24862) with counterpart, shows two lobes of a pinna, one lobe being much puckered and folded longitudinally. The midrib is stout and tapering, rounded and prominent on the lower surface (represented by a furrow on the impression). The nerves are about 0·6 to 0·75 mm. apart where they spring from the midrib. They are represented on the impressions by thin raised thread-like lines. The marginal teeth are well preserved in parts (Pl. 36, figs. 66–68); the margins of the frond were thickened, especially at the tips of the teeth. There is nothing in this specimen, or in V.24861 which also shows teeth, to indicate that the teeth were associated with fallen fertile pinnules as Gardner supposed, and on the whole the appearance of the two specimens is against this interpretation. Nevertheless it is possible that these particular fragments happened to have been barren, whereas if they had been fertile the association of teeth and fertile pinnules might have been shown. But whether the teeth were, or were not, associated with fertile pinnules, it seems clear at least that their presence indicates that in the Woolwich Beds there was a species quite distinct from the Bagshot *L. kaulfussi* with its entire-margined barren pinnules and its much-branched fertile pinnules which apparently were borne in a panicle at the tips of barren fronds and not around their margins. In describing the species Gardner (1886 : 403) recorded that " the pinna was simple or cleft into two or more lobes". The veins were free, diverging at a sharp angle from the midrib, forking once or twice. Prestwich figures nerves about 0·75 mm. apart near their origin on the midrib.

Gardner thought the species indistinguishable from *Lygodium japonicum* Sw. a native of Japan, China, Ceylon, Java and the Philippines, but this is a curious conclusion for it does not accord with his views about the position of the fertile pinnules of the fossil. In living *L. japonicum* they are borne in clusters at the tips of the barren pinnules as they are also in *L. articulatum* Rich. and *L. palmatum* Sw. *L. prestwichii* rather resembles the other group of living species in which the strap-shaped pinnules whether simple or parts of subdivided pinnae carry the fertile pinnules around their margins, an arrangement seen, for example, in the living *L. flexuosum* (L.), *L. volubile* Sw., *L. circinnatum* (Burm.) and *L. salicifolium* Presl.

*Lygodium* is a climbing fern of tropical and subtropical lands in both hemispheres. In North America it occurs in Florida and Massachusetts in woodlands and in lowland areas of New Jersey. In South America it extends to southern Brazil east of the Andes but less far south on the west of the mountain range. Professor Halle (1940) points out that his fossil species *L. skottsbergii* is found 30° south of the present extension of the genus. In the old world the genus goes north into China, e.g. 500 metres above sea level in Szechuan and southward to New Zealand, occurring throughout the whole of the tropical belt. Some species have pinnules with toothed margins and in others the margin is entire.

### ***Lygodium kaulfussi*** Heer

(Pl. 37, figs. 70–83; Pl. 38, figs. 84–87)

1861. ? *Lygodium kaulfussi* Heer, p. 409, pl. 8, fig. 21; pl. 9, fig. 1.
? 1879. *Asplenites prae-allosuroides* Gardner & Ettingshausen, p. 34, pl. 3, figs. 1, 2.
1880. *Lygodium kaulfussi* Heer: Gardner & Ettingshausen, p. 47, pl. 7, figs. 1, 3–8; pl. 10, fig. 11.
1882. *Lygodium kaulfussi* Heer: Gardner, pp. 67, 68.
1886. *Lygodium* sp., Gardner, pp. 401, 404, pl. 3, fig. 9.

DIAGNOSIS. Barren fronds simple or deeply palmately divided, tapering to the base. Fertile pinnules borne in a sympodially branched tuft with segments in pairs or threes. Spores trilete and tetrahedral-globose, shining, smooth or minutely granular, about 75 to 112$\mu$ in diameter.

NEOTYPE. V.14962.

DESCRIPTION. Barren pinnules have been described and figured from Bournemouth and Studland, and two small tufts of fertile pinnules from Bournemouth (Gardner & Ettingshausen, 1879, 1880; Gardner, 1886). Gardner states that the barren pinnules from Studland were very near to those from Bournemouth but with " much closer veins", and suggested that the Studland specimens were intermediate in form between *L. kaulfussi* from Bournemouth and *L. prestwichii* from the Woolwich Beds. It is not clear from his statement whether he really regarded the Studland material as belonging to a species distinct from *L. kaulfussi*. But fertile pinnae with spores now afford evidence that the Studland and Bournemouth material is specifically identical (cf. Pl. 37, fig. 78; Pl. 38, fig. 86 from Branksome Dene, with Pl. 37, figs. 72, 74, 80–83; Pl. 38, fig. 85 from Studland). Moreover, the recently collected barren pinnules from Studland agree closely with some of Gardner's Bournemouth specimens. The differences of nervation which he noted are therefore probably individual variations with no specific significance. This view is supported by the variations which can be found in living *Lygodium* species.

Gardner & Ettingshausen's description of the Bournemouth fronds is full and detailed, and it is not necessary to repeat it, but Gardner gave only the briefest account of the single Studland fragment figured. The following additional details based on the fresh material may therefore not be out of place.

The barren fronds are not infrequently to be found as perishable impressions in the lower part of the soft laminated dark grey clays about 4 to 5 ft. above the sand-rock, i.e. within the lowest 100 ft. of the Lower Bagshot Beds. Often the impressions are covered by decayed remains of actual fronds which quickly crack and crumble on exposure to air. The few pinnules so far seen are variable in shape and sometimes divided near the base (Pl. 37, fig. 70). The lobes may be short or long and lanceolate, obtuse at the apex, tapering somewhat towards the base, with entire margins. The primary nerves are stout but become attenuated above, the secondary nerves are close together, about 0·4 to 0·5 mm. apart, given off at acute angles, thrice forked, sharply defined.

*Fertile pinnules* (Pl. 37, figs. 72–78). The specimen figured from Bournemouth (Gardner & Ettingshausen, 1880, pl. 10, fig. 11) shows a repeatedly divided pinna with stalked pinnules which are linear-elongate and serrate along the margins. Gardner & Ettingshausen (1880 : 48) state that the pinnules in the upper part were " solitary or undivided, but in the lower part two or three occur together or are twice or thrice divided ". This two- or three-fold division may also be seen in the living *L. articulatum* Rich. The midribs are sinuous and the rachides unwinged. Gardner did not record sporangia nor spores, but a preparation from V.14962 (the neotype) has revealed the presence of spores identical with those described below.

In 1882 (p. 68) Gardner reconsidered the specimen which he and Ettingshausen (1879) had named *Asplenites prae-allosuroides* (V.14968), and decided that it was a fertile frond of *Lygodium* with " exceptionally abbreviated pinnules". No spores could be obtained from this specimen when it was re-examined recently, and in view of the difference in form of the fertile segments its identity with *L. kaulfussi* must remain doubtful.

The fertile pinnules from Studland are well preserved. They were isolated from the matrix by boiling, washing and sifting, and were then examined microscopically. Only detached solitary fertile pinnules have as yet been seen. When perfect they are petiolate and, as in the Bournemouth specimens, without any wing-like extension of the lamina along the stalk. They are linear-elongate, obtuse at the apex, serrate along the margins, while the markedly sinuous midrib is sometimes very conspicuous, although only slightly raised, on the upper surface; it is often prominent on the lower surface which may have a longitudinal facet on each side of it (Pl. 37, figs. 73, 75). The epidermis is formed of deeply interlocking cells with beaded appearance due to unevenly thickened walls (Pl. 37, fig. 79). The diameter of the largest cell seen including the digitations was 0·048 mm. The sporangia are oval, flattened, sunk in oval hollows on the underside of the pinnules, concealed by overlapping bracts or indusia. They remain obscure even in macerated specimens because of the thick and opaque character of the bracts and pinnules which surround and protect them. They diverge in a pinnate manner from the midrib, one sporangium corresponding to each tooth of the serrate margin. The walls of the sporangia are usually ruptured so that as a rule the form, structure and annulus are destroyed or masked, especially if covered and surrounded by a mass of liberated spores. After maceration, remains of the annulus can sometimes be seen with thick-walled more or less parallel-sided elongate cells.

*The spores* (Pl. 37, figs. 80–83 ; Pl. 38, figs. 84–87) are numerous, globular-tetrahedral with clear fine triradiate marks, the rays sometimes forking slightly at their free extremities. The surface is shining and smooth or very finely granular resembling figures of *L. skottsbergii* Halle (1940, pl. 1, figs. 9, 10) from supposed Eocene beds of Coronal, province of Concepcion, South Chile, South America. A few tubercles or granules are sufficiently prominent to be visible in profile, but they are probably fragments accidentally adhering to the surface, for although apparent when the spores are first mounted in glycerine, they quickly disappear leaving a perfectly smooth surface. The diameter of the spores varies from 75 to 112$\mu$, and is frequently about 100$\mu$ when uncollapsed, very rarely larger. The thickness of the coat in the largest spore seen was as much as 6$\mu$. More frequently it is only about 3$\mu$ in optical section. The length of the fertile pinnules is about 4·5 mm. ; breadth about 1·5 mm. Length of toothed segments of fertile pinnules about 0·5 mm. Identical fertile pinnules with identical spores were also found at Branksome Dene, Bournemouth Freshwater Beds (Pl. 37, fig. 78 ; Pl. 38, fig. 86).

It must be stressed that barren and fertile material have not yet been found in organic connexion but as their association in the same beds at Studland almost certainly points to derivation from a single species, they are so regarded and described here. The fertile pinnules and spores afford conclusive evidence that the Studland and Bournemouth material is specifically identical, while the barren fronds from the two localities appear to the writer to agree also.

An isolated spore, apparently of this species, has also been found in the Cliff End Beds of Mudeford (Auversian ?) (Pl. 38, fig. 87). Halle (1940: 261) pointed out that the type of *L. kaulfussi* Heer was an indeterminable and useless fragment whereas the numerous fossil records of *L. kaulfussi* are, in fact, based on the well-preserved English Eocene fronds unfortunately identified with the useless Skopau type. Hence, he suggested, Gardner's specimens may, for practical purposes, serve as the type of the species *L. kaulfussi* and the specimen British Museum (Natural History) No. V.14962 is here designated as the Neotype.

The Studland and Bournemouth fossils have been united as a single species only after careful consideration of the evidence afforded by the fertile pinnules from both localities following upon a study of the spores of twenty-six living species. This investigation was made possible by the kindness of Mr. A. H. G. Alston of the Botanical Department, British Museum (Natural History). It strongly suggests that when their characters have been fully studied they will prove to be sufficiently distinctive for use in specific determination in the majority of species. But much time and labour would be required in order to work out the spore characters of the genus in a really satisfactory manner. For in every species it would be essential to examine a wide range of material from different plants and localities to find out the true limits of variation of the spores within each. Moreover the determination of the Herbarium material itself would have to be checked. As an illustration of the nature of the problem it is perhaps sufficient to quote the cases of *L. volubile* Sw. or *L. circinnatum* (Burm.) which displayed considerable variations of spore character on different sheets and which perhaps include more than one species in each case. On the other hand readily recognizable species such as *L. reticulatum* Schk., *L. articulatum*, *L. japonicum*, *L. scandens* (L.), *L. polymorphum* (Car.), *L. smithianum* Pr. and *L. palmatum* Sw., each have distinctive spores which appear constant in character. The spores of different species may vary in form, e.g. they may be more or less conical, or sub-globular, or more or less sharply angled. They also vary in size from about 40$\mu$ in diameter in *L. borneense* and *L. elmeri ;* 40 to 50$\mu$ in *L. japonicum* and *L. polymorphum ;* and 80 to over 100$\mu$ in *L. hians*, *L. articulatum*, *L. reticulatum*, *L. cubense*, *L. merrilli* and *L. lucens*.

Whereas by far the greater number of living species have spores which are ornamented in a greater or lesser degree they do vary considerably in surface ornamentation and thickness of spore wall, while a few species are smooth and shining. Thus *L. elmeri* is smooth and fairly thick-walled with only very occasional scattered minute tubercles. *L. polymorphum* is thin-walled and finely granular all over. *L. reticulatum* has a coarse reticulation of the surface, and *L. scandens* is somewhat similar with a series of deep pits. In *L. articulatum* the whole surface is covered by low, rounded, contiguous tubercles which diminish in size between the arms of the three-rayed scar on the ventral surface. *L. japonicum* is evenly covered with regular, low, rounded, contiguous tubercles smaller than those of *L. articulatum*. *L. borneense* is thin-walled with small distinct close-set tubercles. *L. merrilli* has larger but quite distinctly separated tubercles. In *L. smithianum* and in one sheet attributed to *L. volubile* (Nardil, 1891) from Trinidad, the spore has a fairly broad equatorial flange, irregular scattered large wart-like tubercles sometimes as much as 10$\mu$ broad, with finer tubercles between, especially on the surface in the angles of the rays.

The spores of *L. kaulfussi* from Studland and Bournemouth are characterized by their large size, often 100$\mu$ or larger, thin walls, and smooth or very finely granular surface. These characters combined, together with the globose-tetrahedral shape, appear to distinguish them from any living *Lygodium* seen. As already mentioned (p. 310) smooth-walled spores of exactly similar appearance and comparable size (65–105$\mu$ commonly 85$\mu$) occur in Halle's species *L. skottsbergii*. The fertile fronds of this species appear to have had a mode of growth in a tuft like that of *L. kaulfussi* but show a much reduced lamina on the sides of the rachides, absent (possibly through lack of preservation) in *L. kaulfussi*. Halle separated his species from *L. kaulfussi* on account of the shorter, broader segments of the barren pinnules, their asymmetrical shape and truncate base, and especially on account of the number of segments (three). But he writes that the fertile specimens of *L. skottsbergii* might belong to *L. kaulfussi*. There is certainly a close general resemblance between the two, and this is supported by the character of the unusually smooth spores which are also comparable in size and shape. They are certainly more similar to one another than to any living species, and it is tempting to think that they *may* be identical and that such variations as occur may even be the result of different climatic or ecological conditions.

A few smooth spores and barren and fertile pinnules attributed to *L. gaudini* Heer are figured by Gilkinet (1922 : 5, pl. 14, figs. 2–9). Unfortunately the figures show little detail and spore dimensions are not given. The material is from beds of uncertain age in the argiles of Andenne (Aquitanian or Lower Miocene ?) yielding also a number of Bovey Tracey species. There is no obvious difference from *L. kaulfussi* although Gardner regarded Heer's two species (*L. kaulfussi* and *L. gaudini*) as quite distinct. Possibly in view of Halle's comment on the first named (see p. 311) they should not be separated. It is tempting to wonder whether in view of the preceding remarks *L. kaulfussi* may have been a plant of very wide range, particularly in Eocene times, possibly even a persistent relic of the ancient more or less world-wide genera of the tropical and subtropical province.

While, however, the specific relationship of these forms from wide-spread localities must await further confirmation from an exhaustive comparative study of the actual fossil material, there can be no reasonable objection to uniting the Studland and Bournemouth fossils of which such a study has been made.

The general distribution of *Lygodium* is given on p. 308.

### ***Lygodium poolensis*** n. sp.

(Pl. 38, figs. 88–96)

DIAGNOSIS (based on spores). Spores trilete, subglobular-tetrahedral, ranging from about 50 to 70$\mu$ in diameter, commonly about 65 to 68$\mu$. Depth from the ventral to the dorsal side about 41–42$\mu$. Surface ornamented with numerous flat-topped tubercles about 4μ in diameter below, projecting conspicuously from the surface for about 4μ as seen in optical section.

HOLOTYPE. V.31533.

DESCRIPTION. *Barren pinnules* unknown.

*Fertile pinnules* known only from a single naturally macerated fragment about 1·75 mm. long and from a detached spore on a slide of *Anemia*. Maceration has removed the lamina leaving the slightly sinuous midrib and a few attached solitary sporangia which are borne on it in a pinnate manner at the ends of the nervules. One sporangium (Pl. 38, figs. 88, 89) is perfect, four others are incomplete, two of them being almost entirely broken away. The perfect sporangium is broadly bolster-shaped or sub-ellipsoid with a large spreading annulus on one side near the proximal end. It was very clearly displayed when the specimen was first placed in nitric acid and can still be distinguished when examined by strong reflected light against a white background. The sporangium is about 0·55 mm. long, 0·3 mm. broad. The annulus about 0·34 mm. in maximum diameter extending for over half the length of the sporangium. It is only about 0·17 mm. in depth.

*Spores* numerous, trilete, tetrahedral-subglobose, low conical or low triangular-pyramidal having a sub-circular or rounded triangular outline. Triradiate mark clear, sharp and fine, the rays about 18–25μ in length. Surface highly ornamental having a series of deep pits whose coalescent walls produce the effect of rather flat-topped tubercles (Pl. 38, figs. 90–96). Diameter of tubercles often about 4μ; height 2·5 or 3 to 4μ. About four tubercles occupy a square of about 12·5 × 12·5μ. The tubercles project conspicuously at the circumference of the spores when seen in profile. Typical spore dimensions are 65μ; 70 × 50μ; 65 × 60μ; 55 × 68·7μ; 66 × 50μ; 66 × 57μ; 57 × 54μ; 63 × 48μ. One spore which measured 68·7μ in diameter was 41·25μ in height (dorsi-ventral profile); thickness of spore walls where measured about 4μ.

REMARKS: As already noted there are some grounds for regarding spores of *Lygodium* as of use in specific determination. Tubercled spores similar in character to those of the fossil occur in very few living species but are present in *L. scandens* Sw. and *L. reticulatum* Schk. These two species are grouped together by Diels on account of their reticulated spores which appear to separate them from other species. A sheet of *L. scandens* (Thwaites 1404) in the Herbarium of the Botanical Department, British Museum (Natural History) showed spores varying in diameter from about 66 to 84μ, and in another which more closely resembled the fossil (Ross 123 from Nigeria) spore diameter was 60 to 84μ and the height about 41μ (Pl. 38, figs. 97–101). The tubercles appeared somewhat less conspicuous and prominent at the margin of the spore as well as rather coarser and more rounded than in the fossil. A sheet of *L. reticulatum* (Compton 244) had larger spores, 80 to 110μ in diameter, while another sheet from New Hebrides (McGillivray 1860) showed similar variations of size. The tubercles were considerably less prominent at the margin than in the fossil.

Diels gives the geographical range of *L. scandens* as West Africa, Further India to Chitral, South China, Malaya to North Australia, and of *L. reticulatum* as North Australia, Melanesia and Polynesia. Hence the fossil *L. poolensis* appears to be related to an essentially tropical old world sub-division of *Lygodium*. In *L. scandens* the nerves of the barren pinnules are free ; in *L. reticulatum* they anastomose. A note on the sheet of *L. scandens*, from which spores are illustrated, states that it occurred in swamp forest near sea level in Nigeria. *L. poolensis* is readily distinguished by its spores from the smooth-spored *L. kaulfussi*.

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## PLATE 32

### *Anemia poolensis* n. sp.

Fig. 1. A recurved pinnule with attachment to stipe at (*a*). Several segments are seen directed downwards with the sporangia on the lower surface projecting along their margins. The transverse and longitudinal alignment of the cells over the middle of the segments on the upper surface is clearly seen. × 26. V.31495.

Fig. 2. A single boat-shaped segment of a pinnule, side view with upper surface on the right. It shows the crowded sporangia arranged in two rows on the under surface. × 15 (now disintegrated).

Fig. 3. The same, enlarged. The apical annuli with elongate cells can be distinguished. × *ca.* 35.

Fig. 4. A segment, lower surface with distal end at the top of the figure. It shows the sporangia springing from the pinnule close to the nervule. Annuli of sporangia and elongate cells of sporangial wall and pinnule are visible. × 50. V.31496.

Fig. 5. Segment attached at (*a*), dorsi-lateral view showing the apices of three sporangia which project beyond the margin of the segment. Two have gaped longitudinally. The sporangium at the distal end (top in figure) is shown in Pl. 33, fig. 15. ×28·5. V. 31497.

Fig. 6. A pinnule segment covered with a felt of pointed hairs. Attachment at (*a*). × 50. V.31498.

Fig. 7. A detached sporangium showing the contraction to the attachment and short stalk at (*a*). The dense region of the annulus is visible at the opposite extremity. × 150. V.31499.

Fig. 8. Another with dark thick-celled annulus and attachment (twisted) at (*a*). The thin cells of the sporangial wall show the bead-like thickening which is present on the inner surface × 150. V.31500.

All the above are from Lake, Dorset.

Fig. 9. Apical view of a disrupted annulus with stomium at (*s*). Remains of the torn sporangial wall close to the line of the stomium are seen at (*spg*). × 150. V.31516. Sandbanks, Dorset.

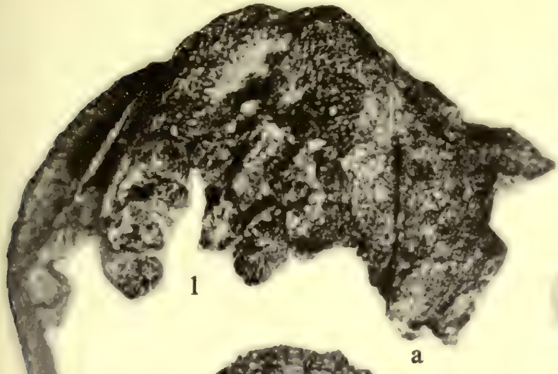
Fig. 10. Apex of a sporangium, side view, showing the thick-walled annulus and some of the contained spores. Granules in the cells of the sporangial wall chiefly below the annulus appear to be chloroplasts. × 150. V.31512. Branksome Dene, Dorset.

### *Anemia gardneri* (Recent)

Fig. 11. Part of a pinna to show the habit, with tertiary reflexed pinnae arising from the stipe and bearing reflexed enrolled pinnules. × 5·5.

Fig. 12. The same, opposite side. × 5·5.

Fig. 13. The same (upper part) to show the recurved pinnules more clearly. × 15.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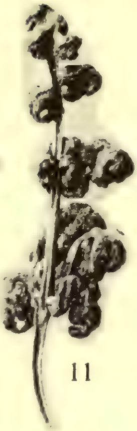
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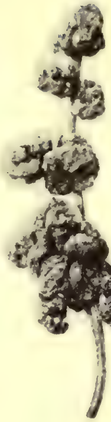
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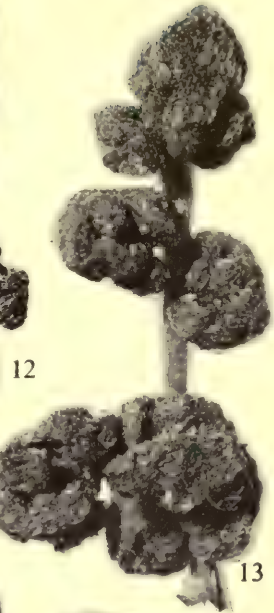
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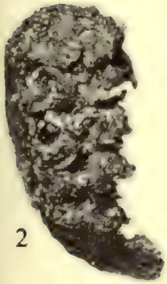
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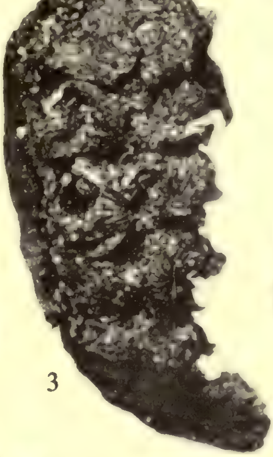
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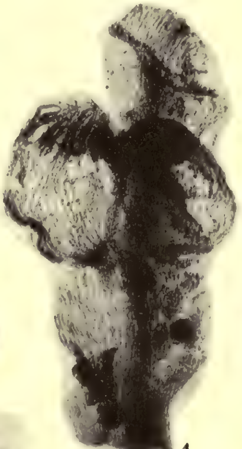
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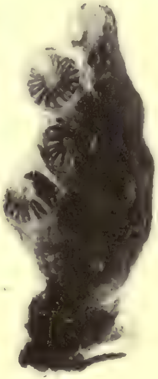
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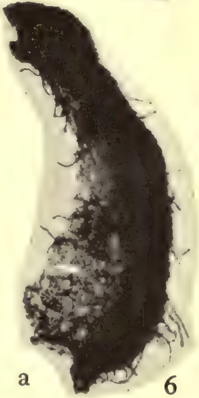
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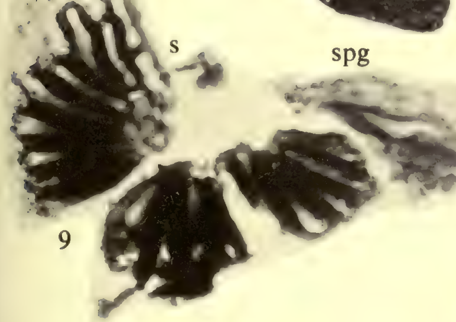
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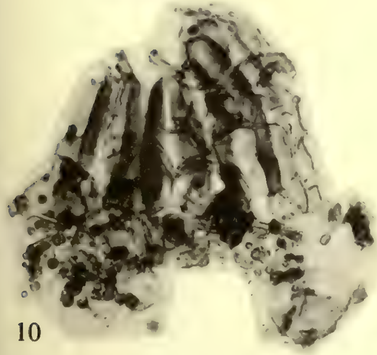
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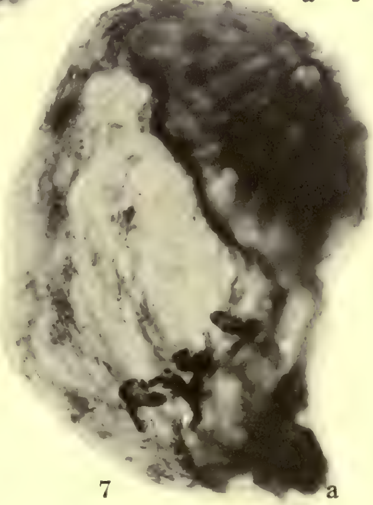
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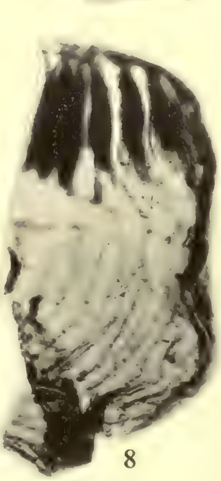
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ANEMIA POOLENSIS A. GARDNERI (Recent)

## PLATE 33

### *Anemia poolensis* n. sp.

Fig. 14. Apex of a dehisced sporangium showing the stomium and the thick-walled annulus. A few cells of the broken apical plate still adhere to the upper ends of the annulus cells. A few cells of the sporangium wall with bead-like thickening are seen at *sw*. × 150. V.31501.

Fig. 15. Apex of a sporangium which has dehisced longitudinally. It shows clearly the ring of thick-walled cells which form the annulus and the thin-walled cells bordering the stomium (*st*). The multicellular apical plate lies between the upper ends of the annulus cells. Spores still remaining within the sporangium are visible at *s*, *s*, *s*. × 161. This sporangium is the topmost one shown in Pl. 32, fig. 5. V.31497.

Fig. 16. The apex (side view) of a sporangium (*sp* 1) of which the apical plate is obscurely seen at (*a*). (*an*) is the thickened annulus. Part of the annulus of another sporangium with its apex to the right is at (*sp*2). × 150. V.31502.

Fig. 17. The sporangium (*sp*1) in fig. 16 showing the cells of the burst apical plate (*a*) between the upper ends of the thickened annulus cells. × 400.

Fig. 18. Part of a pinnule segment. Two paraphyses (*p*, *p*) are still in position on the under surface which faces the camera. × 75. V.31503.

Fig. 19. A detached almost unmacerated paraphysis showing the inflated form and opaque character before maceration. × 400. V.31504.

Fig. 20. Another large detached paraphysis which has begun to collapse and crumple as the result of maceration. The opaque lining has begun to break down as can well be seen at the proximal end (*p*). The point of attachment was at (*a*). × 400. V.31499.

Fig. 21. Another (still opaque) showing the point of attachment below at (*a*). × 400. V.31505.

Fig. 22. Another after treatment, translucent but still inflated although somewhat crumpled. × 400. V.31506.

### *Anemia schimperiana* (Recent)

Fig. 23. A Recent paraphysis for comparison (Gossweiler 9705). × 400.

### *Anemia poolensis* n. sp.

Fig. 24. A spore showing the smooth inflated form and (obscurely) the three rays. × 400. V.31507.

Fig. 25. Another, partly out of focus, showing two of the three rays clearly. The smooth inflated form is again shown. × 400. V.31505.

Fig. 26. The same spore with different focus. The thickness of the wall and smooth rounded form are indicated. The rays are out of focus. × 400.

Fig. 27. Another spore showing the triradiate mark. The forking of the free ends of the rays is clearly visible. × 400. V.31508.

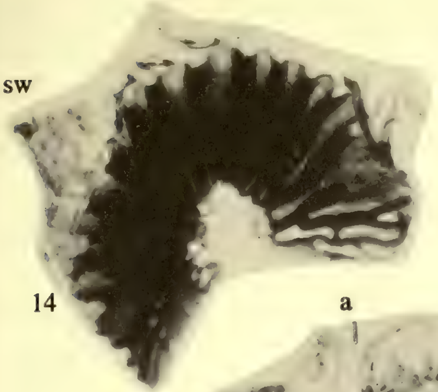
All the above, except fig. 23, are from Lake, Dorset.

Fig. 28. A spore slightly collapsed showing the three rays along one of which the spore has burst. × 400. V.31517. Sandbanks, Dorset.

Fig. 29. A spore showing the three rays very clearly. × 400. V.31513. Branksome Dene, Dorset.

Fig. 30. A somewhat crumpled spore. × 400. V. 31513. Branksome Dene, Dorset.

Fig. 31. A somewhat crumpled detached spore almost certainly of this species. × 400. V.31518. Alum Bay, Isle of Wight.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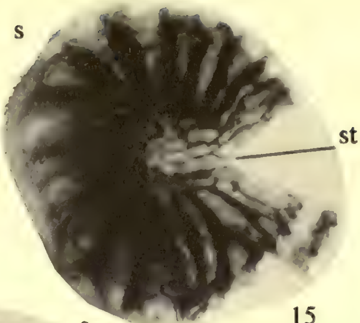
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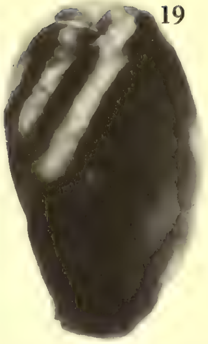
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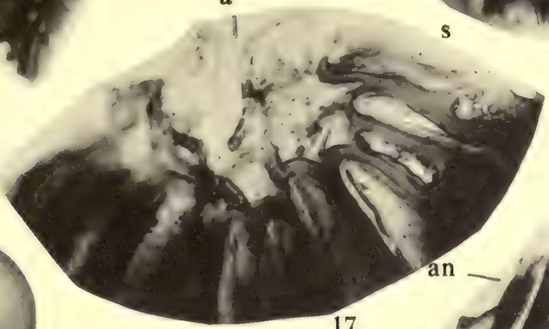
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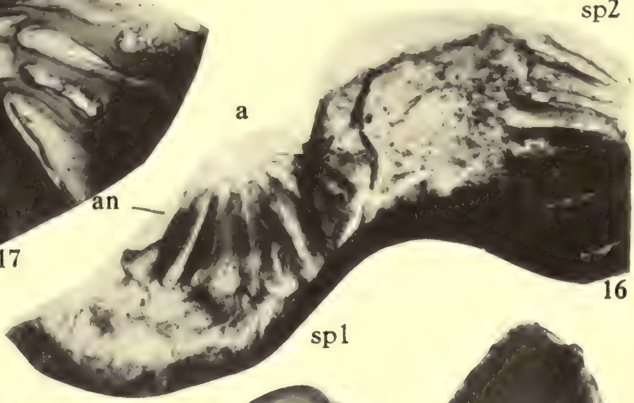
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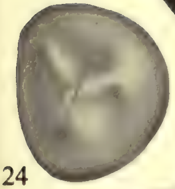
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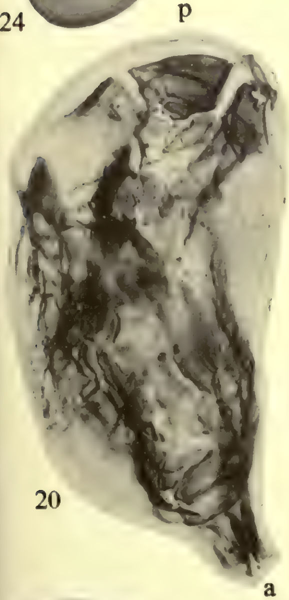
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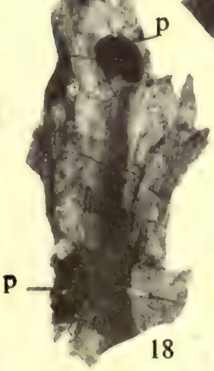
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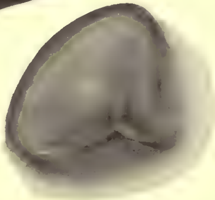
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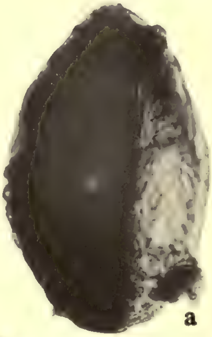
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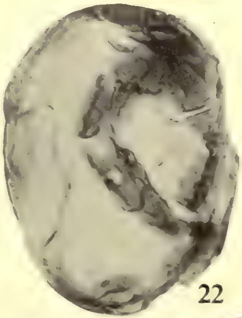
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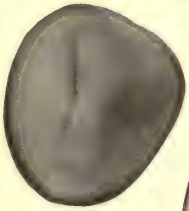
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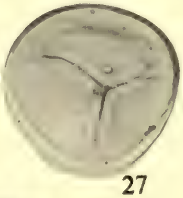
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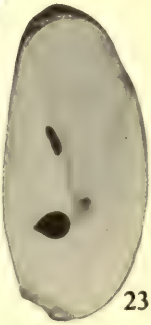
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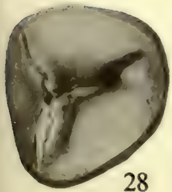
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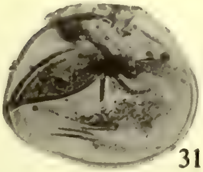
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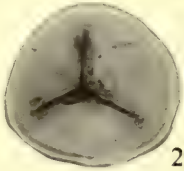
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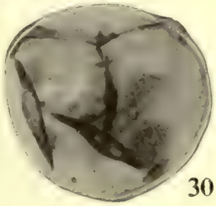
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ANEMIA POOLENSIS, A. SCHIMPERIANA (Recent)

## PLATE 34

## *Anemia poolensis* n. sp.

FIG. 32. Microtome section through a pinnule segment showing more than one layer of thin-walled cells. × 150. Section now disorganized. V.31509.

FIG. 33. Microtome section across a recurved fertile pinnule. It shows the overlapping of pinnule segments, sporangia packed with spores close together on the lower surfaces of the segments, and the thick-walled cells of annuli usually in section. × 50. V.31510.

FIG. 34. Part of another section across the same pinnule. Two overlapping segments are shown, many cells thick in this part of the pinnule. One sporangium in section and parts of two others, one with annulus displayed. × 150.

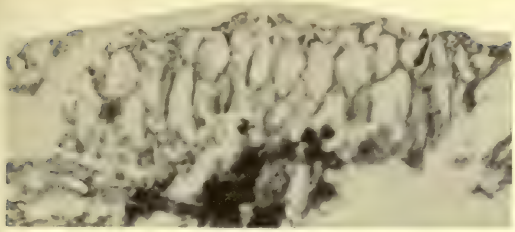
FIG. 35. Another microtome section showing the annuli and spores of two sporangia. × 150. Section now disorganized. V.31509.

FIG. 36. Microtome section showing thickened tracheids in the pinnule segment. Part of an annulus is seen below. × 400. V.31506.

FIG. 37. Another section of the same pinnule showing overlapping pinnule segments, many cells thick proximally, thinning to a few cells thick only, distally. A partly collapsed paraphysis (*p*) is seen arising from one of the segments. Two sporangia are visible in section, that on the right showing much of the annulus. Below it is a small patch of chloroplast granules (*chl*) probably inside one of the cells of the sporangium wall. Spores are visible in the sporangia. × 150. V.31506.

FIG. 38. Part of the same, enlarged, to show the group of chloroplasts just below the thick-walled cells of the annulus. × 400.

All the above are from Lake, Dorset.



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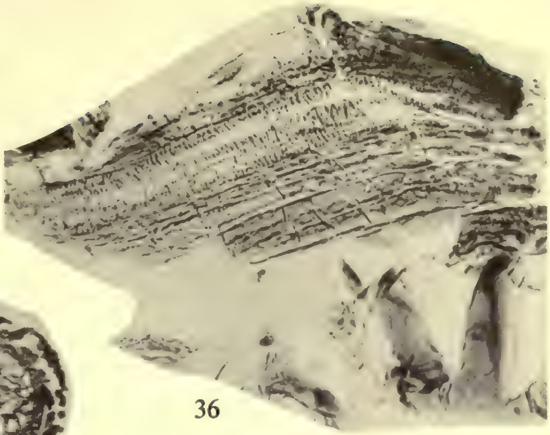

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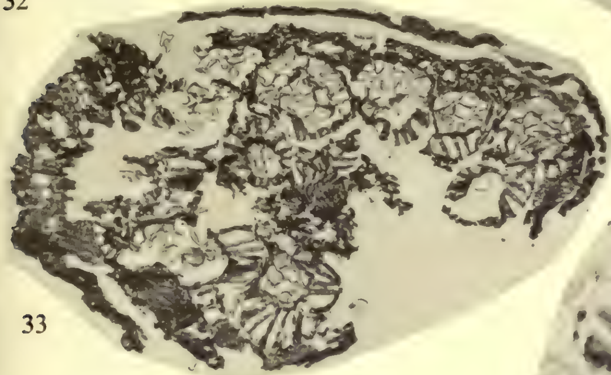

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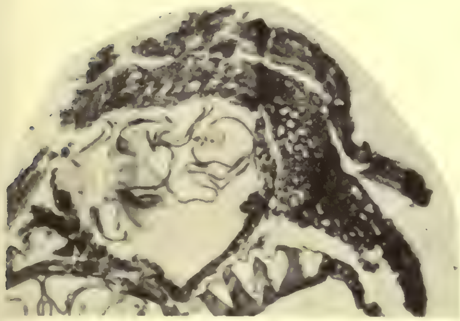

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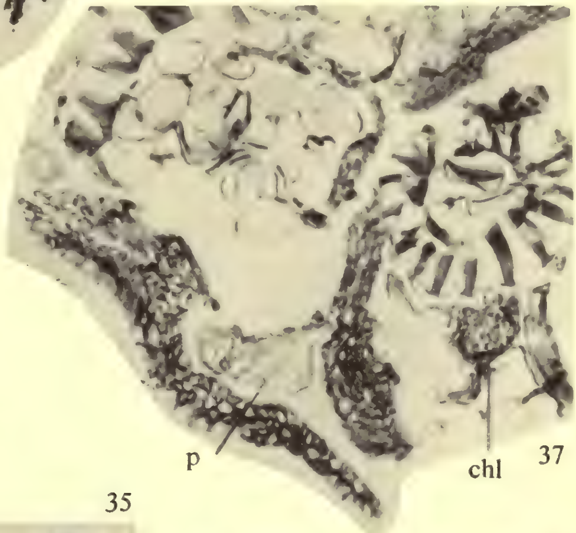

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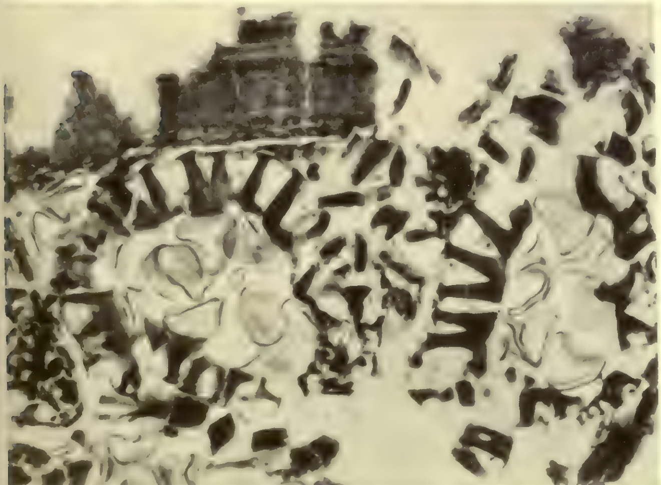

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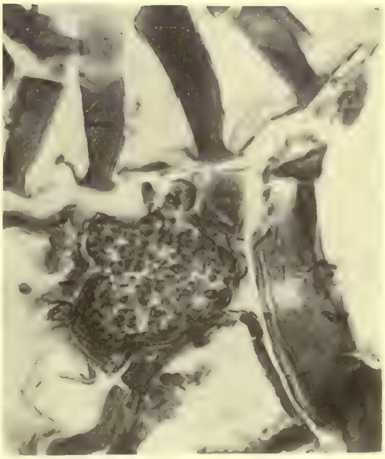


ANEMIA POOLENSIS

## PLATE 35

### *Anemia colwellensis* n. sp.

FIG. 39. Annulus, imperfect, from above. × 150. V.31519.

FIG. 40. Part of another annulus, torn and distorted, from above. × 150. V. 31520.

### *Anemia poolensis* n. sp.

FIG. 41. Annulus, from above, for comparison. The cells which have the appearance of an apical plate are probably a displaced fragment of sporangial wall. Each shows one dark spot (chloroplast?). × 94. V.31514. Branksome Dene, Dorset.

### *Anemia colwellensis* n. sp.

FIG. 42. Upper half of a sporangium with apical annulus, side view. Two or three cells of the apical plate remain. The cells of the sporangium wall immediately below the annulus show numerous opaque grains of pyrites, perhaps pyrites replacements of chloroplasts. × 94. V.31521.

FIG. 43. An enlargement of the same. (*ap*) cells of apical plate. × 150.

FIG. 44. A somewhat distorted sporangium, side, showing the apical annulus above, and the torn sporangium wall below. × 150. V.31520.

FIG. 45. Remains of two sporangia (*sp* 1, *sp* 2) seen from the side. In both the annulus is dense and black, their cells being almost indistinguishable. The thinner sporangium wall is preserved below the annulus in one specimen (*sp* 2) only. A few pyrites grains (chloroplasts?) are seen. Spores are visible at (*s*, *s*). × 150. V.31522.

FIG. 46. An annulus, from above. The ring of cells is ruptured and the apical plate destroyed. A spore is seen in the gap. × 150. V.31520.

FIG. 47. A paraphysis (*p*) still attached to a fragment of leaf. × 400. V.31520.

FIG. 48. Another isolated paraphysis. × 400. V.31520.

FIG. 49. A spore showing the ridges. × 200. V.31522.

FIG. 50. The same (partly reflected light) showing the straight untubercled character of the ridges. × 400.

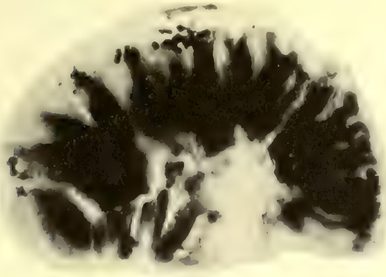
FIG. 51. The same (transmitted light) focused to show the triradiate mark. × 400.

FIG. 52. The same focused to show spore outline and thickness of wall. × 400.

FIG. 53. Another spore, side view. × 400. V.31522.

All the above, except Fig. 41, are from Colwell Bay, Isle of Wight.

All specimens of *Anemia colwellensis* are from the holotype.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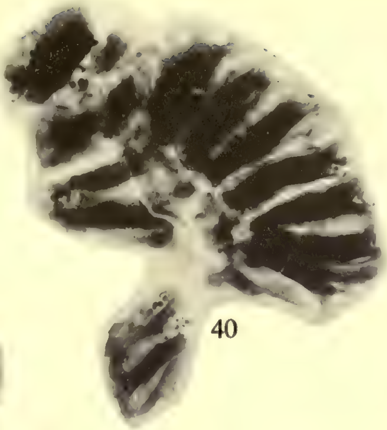
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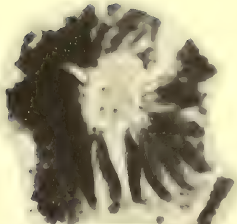
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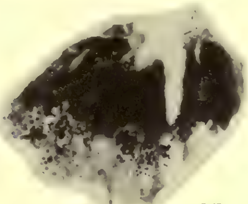
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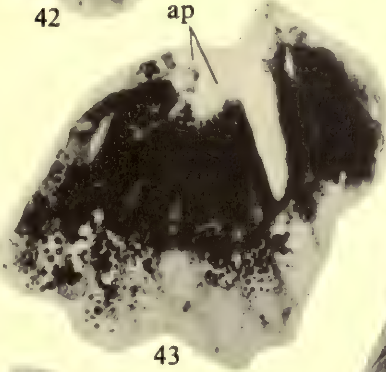

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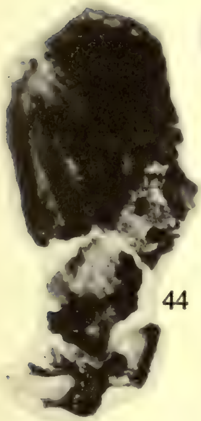
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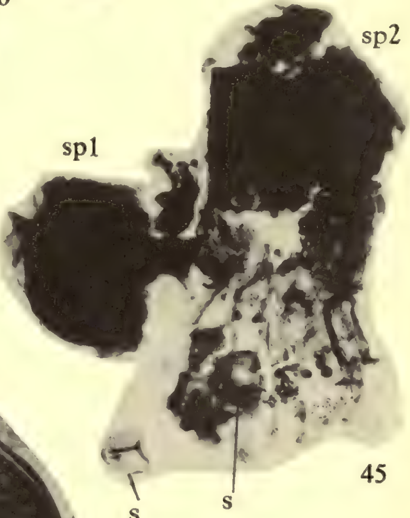

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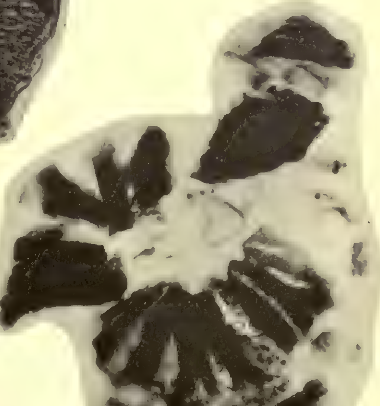
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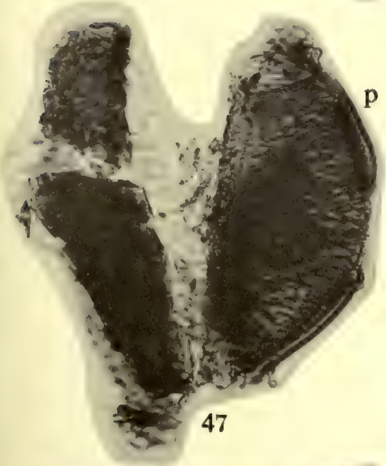

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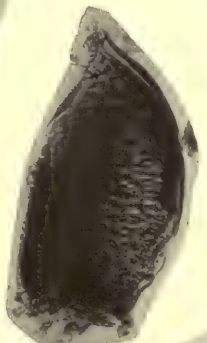
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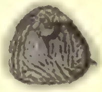
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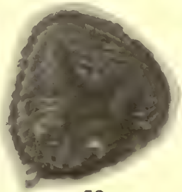
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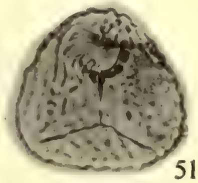
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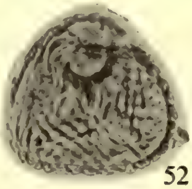
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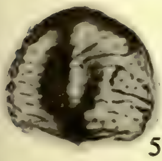
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ANEMIA COLWELLENSIS, A. POOLENSIS

## PLATE 36

### *Anemia poolensis* n. sp.

FIG. 54. A spore showing the smooth outline and triradiate mark with one forked distal end. Another spore is seen obscurely out of focus behind. × 400. V.31508.

FIG. 55. Another spore showing outline and smooth surface. × 400. On this slide entrapped among the hairs of *Anemia poolensis* is a single spore of *Lygodium poolensis*. V.31511.

FIG. 56, 57. Two similar spores. × 400. V.31508.

All the above are from Lake, Dorset (Extracted from pinnules).

FIG. 58. A spore showing obscurely the triadiate mark. × 400. V.31515. Branksome Dene, Dorset.

### *Anemia colwellensis* n. sp.

FIG. 59. A spore somewhat collapsed showing ridged surface. × 200. V.31522.

FIG. 60. The same spore. × 400.

FIG. 61. Another spore showing the "beaded" effect where the ridges on two surfaces cross one another. × 400. V.31522.

FIG. 62. Another spore showing outline and thickness of wall. It has gaped along two rays of the triradiate mark. × 400. V.31523.

FIG. 63. Another showing a ridge branching and the rather obscure triradiate mark. × 400. V.31522.

FIG. 64. Another, side elevation, showing ridges obscurely. The spore has partly folded and collapsed. × 400. V.31523.

All the above are from Colwell Bay, Isle of Wight.

### *Anemia* sp.

FIG. 65. Two impressions of barren pinnules. The nervation is comparable with that seen on the fertile pinnule of *A. colwellensis*. × 2. V.17498. Thorness Bay, Isle of Wight. Also figured Reid & Chandler, 1926, pl. 1, fig. 11.

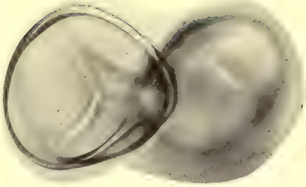
### *Lygodium prestwichii* Gardner

FIG. 66. Impression of the upper surface of a bilobed pinnule, one lobe well exposed, the other, rolled up, at *l*2. The toothed margin is seen on the left of the larger lobe. The secondary nerves. sunk in the original, appear as fine thread-like ridges, the primary nerve appears as a sharp ridge in the impression representing a sharply angled channel in the original. × 2. V.24862. Newington, Kent.

FIG. 67. The counterpart of the above showing the impression of the lower surface with conspicuous rounded midrib in the original (a rounded channel in the fossil) and the raised thread-like impressions of the sunk secondary nerves of the original. Second lobe of leaf at *l* 2. × 2.

FIG. 68. The teeth on the right margin in Fig. 67. The thread-like secondary nerves are also seen and the thickening of the margin. × 6·5.

FIG. 69. An impression of the lower surface of another pinnule with well-preserved nerves but poorly preserved margins scarcely showing the teeth. × 2. V.24859. Newington, Kent.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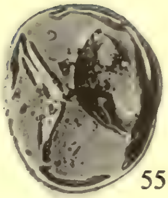
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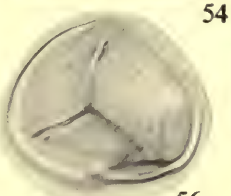
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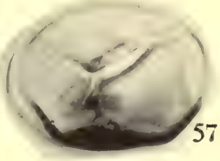
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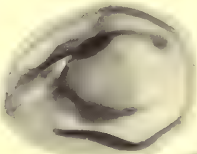
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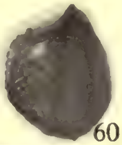
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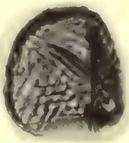
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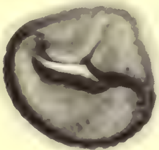
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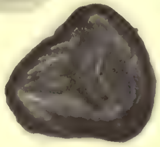
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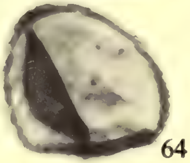
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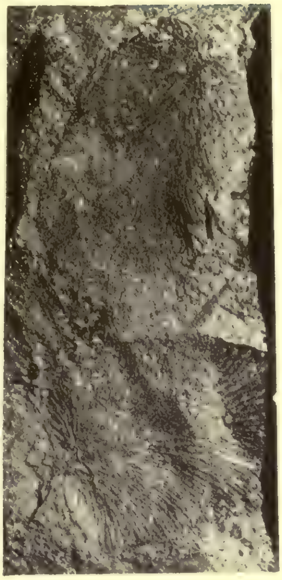
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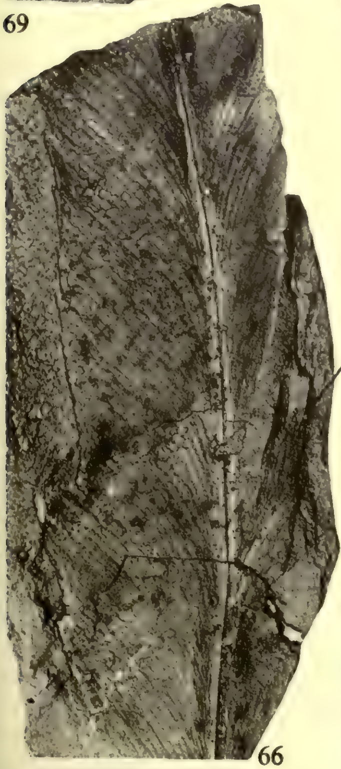

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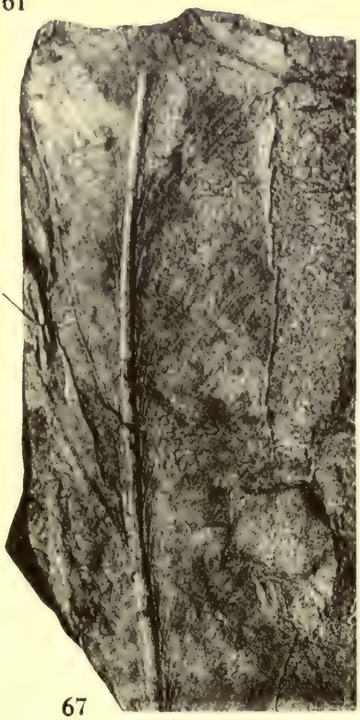
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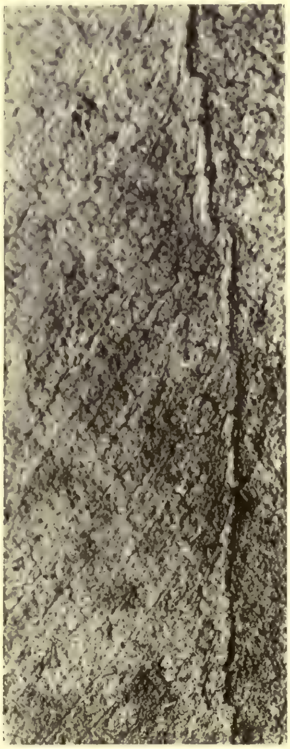
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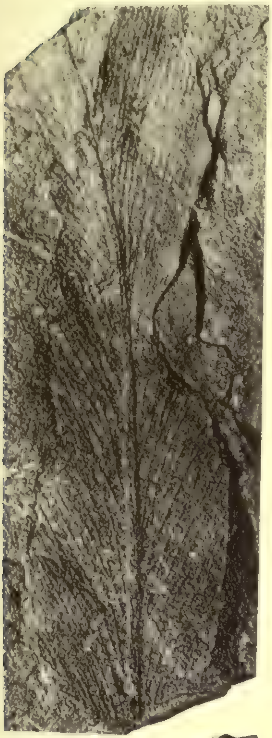
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ANEMIA POOLENSIS, A. COLWELLENSIS, ANEMIA SP., LYGODIUM PRESTWICHI

## PLATE 37

### *Lygodium kaulfussi* Heer

FIG. 70. Impression of a barren-lobed pinnule showing nervation and entire margin. × 1·8. V.28659.

FIG. 71. Another long narrow pinnule lobe. × 1·8. V.28658.

FIG. 72. Fertile pinnule, upper surface. × 15·5. V.31524.

Fig. 73. The same, lower surface. × 15·5.

FIG. 74. Another fertile pinnule (incomplete at the base), upper surface. × 15·5. V.31525.

FIG. 75. The same, lower surface. It shows clearly the marked sinuosity of the midrib. × 15·5.

FIG. 76. A distorted fertile pinnule showing the long stalk. × 15·5. V.31526.

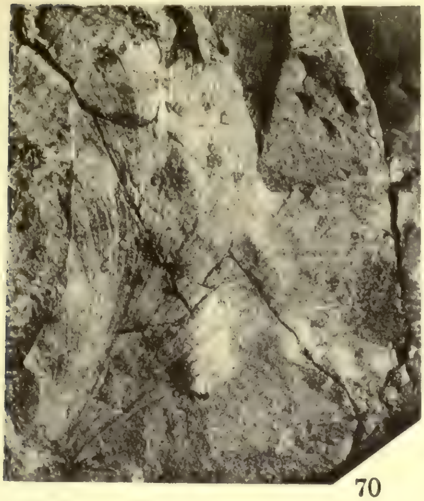
FIG. 77. The same, opposite side. × 15·5.

Fig. 78. A fertile pinnule, upper surface, somewhat battered and sand pitted. × 15·5. Specimen destroyed in macerating to release few remaining spores (slide V.31531). Branksome Dene, Dorset.

FIG. 79. Cuticle fragment from a fertile pinnule showing sinuous cells and " beaded " thickening, giving a " dotted " effect. × 150. V.31527.

FIGS. 80–83. Typical spores extracted from two fertile pinnules, showing the smooth surface and triradiate mark. Folds shown are due to partial collapse. × 400. Figs. 80, 81 are from V.31528. Figs. 82, 83 are from V.31529.

All the above, except Fig. 78, are from Studland, Dorset.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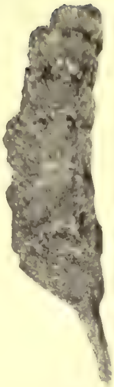
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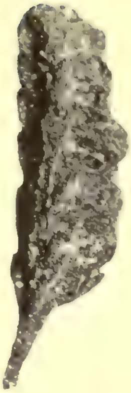
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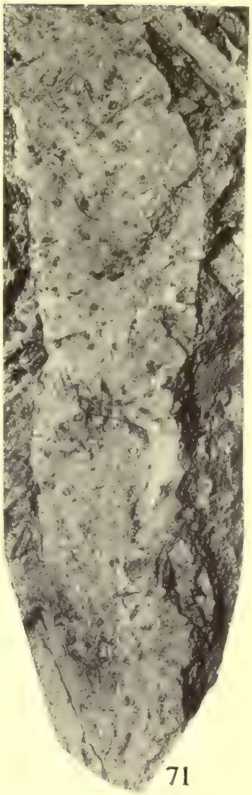
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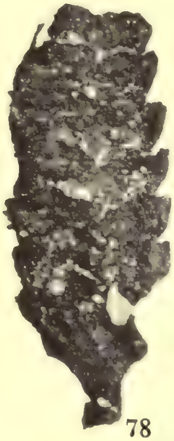
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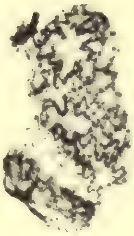
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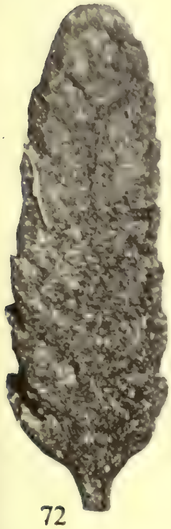
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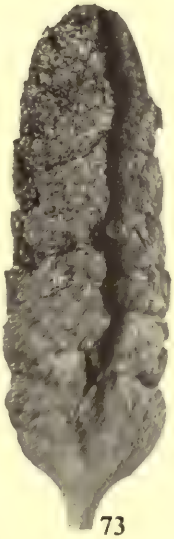
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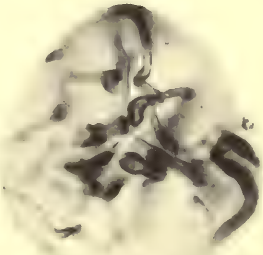
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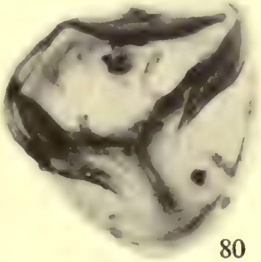
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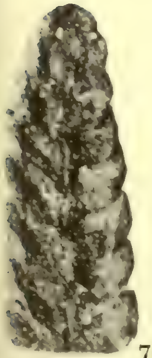
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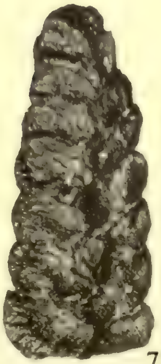
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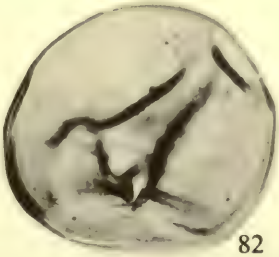
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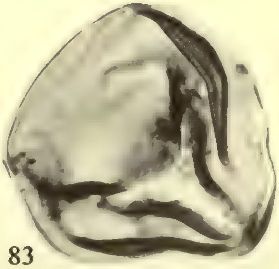
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LYGODIUM KAULFUSSI

## PLATE 38

### *Lygodium kaulfussi* Heer

FIG. 84. An unusually large and thick-walled spore extracted from one of the fertile pinnules. It has burst along the triradiate mark. × 400. V.31530. From the pinnule which yielded the spores figured in Pl. 37, figs. 82, 83 (V.31529).

FIG. 85. A typical spore showing the smooth surface and triradiate mark. Folds are due to collapse. × 400. V.31528. The spores in Pl. 37, figs. 80, 81 are from the same pinnule.

Both the above are from Studland, Dorset

FIG. 86. A large spore removed from the fertile pinnule (Pl. 37, fig. 78) showing the smooth surface and triradiate mark and small fork at the termination of the ray at the top of the figure. × 400. V.31531. Branksome Dene, Dorset.

FIG. 87. A collapsed isolated spore apparently of this species. × 400. V.31532. Cliff End, nr. Mudeford, Hampshire.

### *Lygodium poolensis* n. sp.

FIG. 88. A naturally macerated fragment of fertile pinnule showing the recurved sporangia exposed by the decay of the enveloping pinnule segments and bracts. Only one (x) is complete. This one shows the annulus by reflected light. *r*, *r* remains of other sporangia. × 50. V.31533. Holotype.

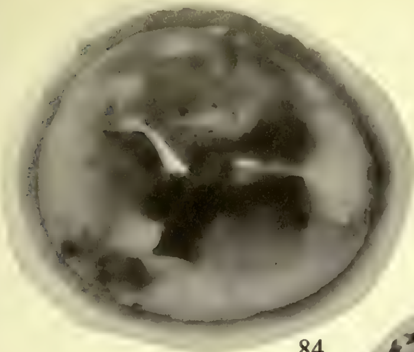
FIG. 89. Diagram of the sporangium (*x*) in Fig. 88 to show the position of the annulus which is very obscurely seen in the photograph.

FIGS. 90–96. Four spores from the above fertile pinnule. They show the deeply pitted surface (the pits bounded by the walls of confluent tubercles?). Figs. 95, 96 represent the same crushed spore. Fig. 95 is focused to show the thickness of the wall, Fig. 96 the extent of the triradiate mark. Figs. 90, 91 and 94 also show the triradiate mark. Figs. 92–94 represent the same spore differently focused to show triradiate mark, outline and surface ornamentation. Pits show best in Fig. 93, tubercles forming the walls of pits in Fig. 92 (top right). All × 400. V.31534–36.

All the above are from Lake, Dorset.

### *Lygodium scandens* Sw. (Recent)

FIGS. 97–101. Spores. Fig. 97 shows a crushed spore which has split along the triradiate mark. Fig. 98, the triradiate mark in an uncrushed spore. Fig. 99 is the same as Fig. 98 but the focus shows the wall thickness and pitted surface. Fig. 100, another spore showing surface structure and pitting. Fig. 101, another focused to show wall thickness in optical section. It also shows obscurely the triradiate mark. Figs. 97, 99–101. × 400. V.31537. Fig. 98. × 400 approx. Recent (Ross 123. Nigeria).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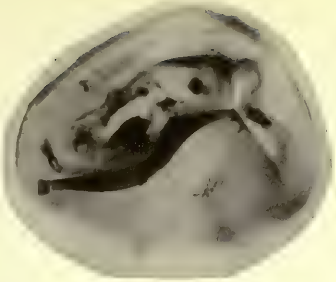
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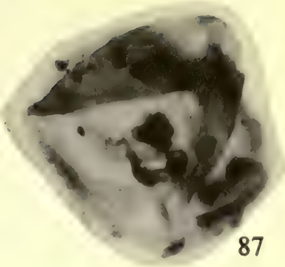
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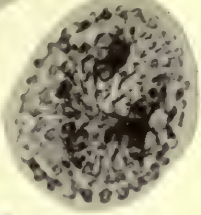
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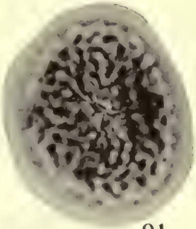
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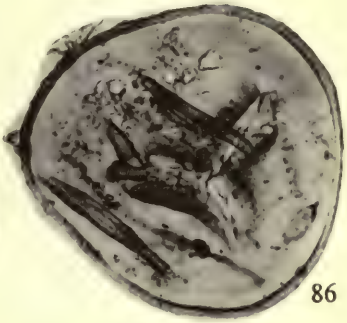
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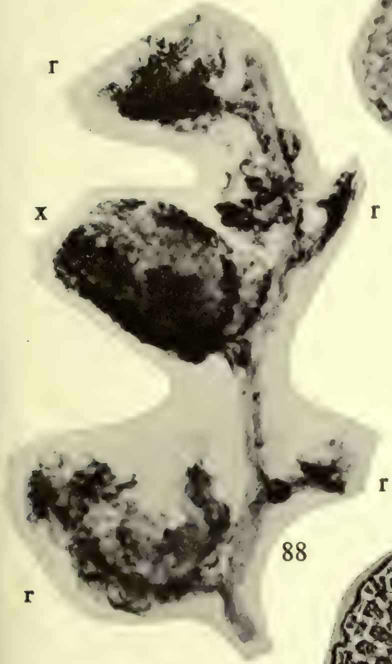

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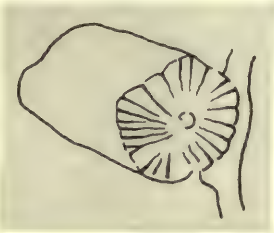
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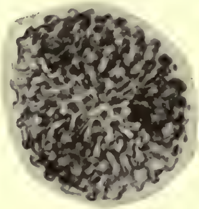
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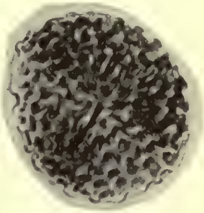
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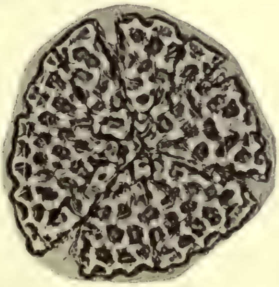
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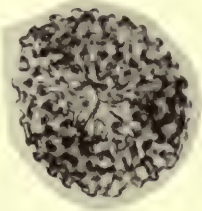
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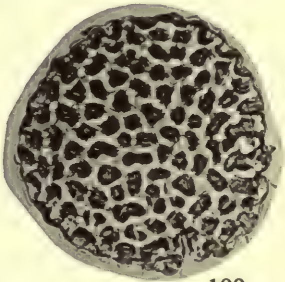
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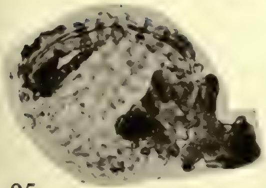
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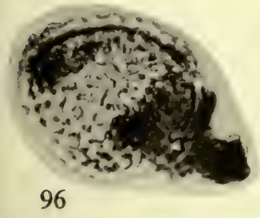
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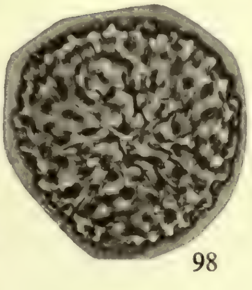
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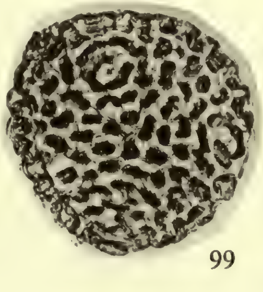
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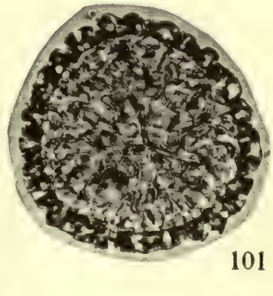
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# THE BRACHYOPID LABYRINTHODONTS

D. M. S. WATSON

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
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*By* D. M. S. WATSON

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## INTRODUCTION

THE amphibia now known as " Labyrinthodonts " were first mentioned in print in G. F. Jaeger (1824 : 10), who, in 1828, published figures of three teeth called *Mastodonsaurus*, two " vertebrae " (which are intercentra), and a pair of exoccipitals held together by parasphenoid which he named " *Salamandroides giganteus* ". Later he recognized that teeth and skull fragments were from the same animal, whose correct name was *Mastodonsaurus giganteus*.

In 1841 R. Owen obtained a tooth of *Mastodonsaurus* and showed (1842) that in section it had a dentine of unique complexity, found also in fragments of teeth from Warwick. He called both materials " *Labyrinthodon* ". This generic name is an absolute synonym of *Mastodonsaurus*, but it may well be retained in the name of a group of higher rank.

During this decade Labyrinthodonts were described in considerable numbers from the Permian and Trias of Germany and Russia, and the next ten years added Canada, India, Australia and South Africa to their known distribution, and extended it downward to the Coal Measures. Thus by 1918 not only had a very large number of Labyrinthodonts been named, but other groups of Palaeozoic amphibia had been established, and a great number of new animals attributed to one or other of them. But the one hundred and twenty-three genera listed in the third edition of Zittel's *Grundzüge* by Broili were scattered amongst a number of major groups without real evidence, and nothing was known of the evolutionary history of any of them. The best summary was that by O. Abel in *Die Stämme der Wirbeltiere*, 1919.

In 1912 I gave a short account of some features of the skulls of two Labyrinthodonts from the Middle Coal Measures showing that the two, though clearly not closely related, agreed in many fundamental characters, including a single basioccipital condyle, reptile-like basipterygoid processes, pterygoids which so closely approach the middle line as to leave only slits as interpterygoid vacuities, and a narrow parasphenoid sheathing closely an interorbital septum. These qualities are largely those of *Seymouria*, and of Reptiles, but they are also found in the Osteolepid fish *Megalichthys*.

In 1919 I reviewed the Permian and Triassic Labyrinthodonts of the world and showed that they had vertebrae which had separate neural arches, pleurocentra and intercentra in Rhachitomi—the pleurocentra vanishing in certain late forms, the " Stereospondyli ". However, the pattern of the dorsal surface of the skull, the lower jaw, clavicular arrangement, scapulo-coracoid, pelvis and proximal limb bones do not enable an animal to be referred to one or other group, though they are diagnostically Labyrinthodont.

Thus I was enabled to take the great mass of Labyrinthodonts of Permian and Triassic time together, and by comparing all known Lower Permian with all known Upper Triassic forms it became clear that the Labyrinthodonts display the following " advances " :

(1) A gradual flattening of skull and body.

(2) A gradual reduction of the basioccipital and its retreat from the condyle.

(3) A reduction of the basipterygoid articulation and its functional replacement by a sutural attachment of an enlarged parasphenoid to the pterygoid.

(4) The exoccipitals extend to form the whole occipital condyle, reach forward to the pterygoids below the ear, and up to sutures with the new occipital flanges of the dermosupraoccipitals and tabulars.

(5) Reduction and final disappearance of cartilage bones in the paroccipitals, proötics, supraoccipital, as well as in the basisphenoid and basioccipital.

(6) An exaggeration of the interpterygoid vacuities and a reduction and shortening of the palatal ramus of the pterygoid.

(7) A reduction of the suspensory part of the skull so that the quadrate condyles come to lie in front of the occipital condyle.

Subsequently, in 1926, I was able to describe good material of several large Coal Measure Labyrinthodonts belonging to the two groups of Loxommids and Anthracosaurs. These animals, although they evidently differ a good deal from one another, agree in many features ; they have a single nearly circular occipital condyle to which the small exoccipitals contribute ; the supraoccipital is bony ; there are no occipital flanges of the tabulars and dermosupraoccipitals ; the basisphenoid has small basipterygoid processes, with articular faces for the pterygoid (and epipterygoid) ; the parasphenoid has a narrow ramus cultriformis sheathing the lower edge of an interorbital septum ; the pterygoids meet one another in front, and leave only narrow slits as interpterygoid vacuities ; the quadrate condyles lie far behind the occiput. In fact in all these respects they represent a logical starting point for the series of evolutionary changes deduced from observation of the then known later Labyrinthodonts. And they evidently make a real approach to the structure found in Osteolepid fishes.

At that time it seemed obvious that further progress required the adequate description of many other Labyrinthodonts, often named but not giving evidence about matters of importance. Dr. M. C. Steen therefore began a study of the faunas of fossil amphibia from the Coal Measures of Nýřany, Bohemia ; Linton, Ohio ; and the erect trees of South Joggins, Nova Scotia. In a series of papers 1931–1938 she revised these faunas, immensely increasing our real knowledge of them. Simultaneously A. S. Romer independently revised the Linton fauna, his results agreeing generally with those of Dr. Steen.

These re-examinations recognized in the Linton fauna a large number of animals with an incomprehensible vertebral column, which were referred to the Phyllospondyli, together with an obvious Loxommid, and *Leptophractus*, not yet adequately known. When in 1937 Dr. Steen examined the Lower Permian *Acanthostoma*, which is certainly a Labyrinthodont, she discovered that it possessed paired pleurocentra and intercentra, which were directly comparable to those of the Linton " Phyllospondyli ", and referred them to the Labyrinthodontia as " Rhachitomi ". Thus the rhachitomous stage of Labyrinthodont evolution was shown to have occurred in Coal Measure rocks in Europe and North America, but at a horizon clearly considerably higher than that of the Newsham and Scottish Coal Measure localities which produced Loxommids and Anthracosaurs. Finally Dr. Steen described a series of small closely related Labyrinthodonts from South Joggins of an age which is considerably older than that of the Linton and Nýřany faunas. It is, however, to be noted that *Eugyrinus wildi* (A. S. W.), which I held to be a Branchiosaur, is now regarded by Romer as a " Rhachitomous " Labyrinthodont. Its skull is in fact, though only 18 mm. in length, very much like that of the Dendrerpetons (cf. Text-figs. 29–31 of *Platystegos*). Indeed it is the only other form to show the peculiar arrangement whereby the squamosal is attached to the supratemporal by a special inwardly directed process. It has enlarged interpterygoid vacuities, relatively larger than those of *Dendrerpeton*, and is the oldest Labyrinthodont (or indeed amphibian) to show them. It has much cartilage bone and is presumably adult.

In 1931 G. Säve-Söderbergh, at the age of 21, collected from rocks in East Greenland, then held to be of Upper Devonian age and certainly containing fish of Old Red Sandstone type, a series of skulls of amphibia of entirely unknown type. He published a preliminary description of these fossils in 1932 and called them the Ichthyostegids. Further materials were collected in later years, but the prolonged illness and death of Säve-Söderbergh prevented any further preparation and description of them. At last in 1952, twenty years after the original description, Dr. Jarvik gave us an admirable account of the tail and hind limb of *Ichthyostega*, a set of new restorations of the skull of that animal, and a short account of a new, related, though very different animal—*Acanthostega*.

Thus it was clear that the whole group of Labyrinthodonts deserved re-examination. The general scheme of evolution I had described was based on gross comparisons of faunas of successive age, and it was obviously necessary to attempt to trace individual evolutionary lines through as long periods as possible, and in considerable detail. This I had begun, but was unable to complete, so that the appearance in 1947 of a great review of the Labyrinthodontia by Professor A. S. Romer was most valuable. Romer made no formal classification, nor did he attempt to isolate individual evolutionary lines, but he brought the small Labyrinthodonts of Linton, Nýřany, and elsewhere into his account in an admirable and illuminating manner.

The present paper is an attempt to isolate a single evolutionary group, long lived, elaborate and world wide, but always recognizable by special structural details found nowhere else. I have work in progress, in a relatively advanced stage, on the immense material of the Capitosaur series.

In 1915 Robert Broom examined the British Museum type skulls of Owen's *Brachyops laticeps* (1854) and Huxley's *Bothriceps australis* (1859). He had himself described *Batrachosuchus browni* (1903), and now pointed out the resemblance between these three animals, founding for them a new family—Brachyopidae—without giving any distinctive characters of the group.

In 1919 I described the structure of the posterior part of the palate of *Bothriceps*, and gave a more complete account of the skull of *Batrachosuchus*. With these forms I brigaded Jaekel's genus *Plagiosaurus* (1914), founded for *P. depressus* from Halberstadt, to which he had added Fraas's *Plagiosternum pulcherrimum* (1913) and Fraas's *Plagiosternum granulosum* (1889), Jaekel having made for these three forms an " order " Plagiosauri, without giving any definition of the group.

I defined the group by saying that its members resemble one another, and differ from all known Stereospondyl types, in the following ways :

(1) The broad parabolic skulls with large anteriorly situated orbits.

(2) The unusual way in which the proötic flange of the squamosal wraps round the outer side of the quadrate, and having formed a laterally concave face on the occipital surface, ends in a ridge, separated from an exactly similar ridge of the pterygoid by the quadrate.

(3) The upturning of the lateral wings of the pterygoids from the subtemporal fossae, so that the palate forms a broad ∩-shaped arch.

(4) The unusual way in which the posterior edge of the pterygoid is applied to the inner face of the quadrate.

(5) The occipital condyles lie far behind the dermosupraoccipitals so that the occipital surface slopes forward.

I pointed out that the then undescribed *Dvinosaurus* possessed all these five qualities, but was a primitive rhachitomous form. No subsequent author (except Sushkin, 1936) appears to have paid any attention to the list of diagnostic characters of the Brachyopids set out above, perhaps because I did not publish a series of drawings illustrating the matter.

Subsequently *Dvinosaurus* was described and figured by Amalitzky (1924), by Sushkin (1923, 1936), and by Bystrow (1935, 1938), the last two bringing out the neoteny which it shows, and the last producing an admirable account of the whole skeleton.

The later Brachyopids have been described and discussed by von Huene (1922) and Tage Nilsson (1934, '37, '39, '45), and A. S. Romer has treated them in his *Review of the Labyrinthodontia* (1947). He accepts the Brachyopidae and the group Plagiosauridae for the extreme forms, but adds the Metoposaurs to the assemblage, whilst removing *Dvinosaurus* to the neighbourhood of *Trimerorhachis* and " *Saurerpeton* ". There is thus some variety of opinion about the whole matter and further treatment of it is necessary.

The Brachyopids proper are rare animals known usually from the occurrence of single individuals of each species from rocks of Upper Permian and Lower Triassic age in Australia, India, South Africa and Argentina, and the published accounts of their structure are inadequate.

## BRACHYOPIDS PROPER

### SURVEY OF GROUP

The Brachyopids include a terminal group of Middle and Upper Triassic forms, the Plagiosauridae, but its typical members are from earlier beds whose age relations are unfortunately not very accurately known. The complete list of these is as follows :

(i) *Brachyops laticeps* Owen. The type—and only known specimen—was found in the " Mángali beds " at Mángali, in Nagpur, Central India. This horizon is assumed on poor evidence to be equivalent to the Panchets (C. S. Fox, 1931 : 159). The age of the Panchets is to be determined from their fauna of vertebrates, and from a considerable flora. The fauna has recently been described by von Huene (1942) who recognizes in it a genuine *Lystrosaurus* and remains of *Chasmatosaurus*, genera otherwise known only in the Lystrosaurus zone of South Africa and of Sinkiang. Furthermore he has described a skull of the Labyrinthodont *Gonioglyptus*, which genus occurs in the Panchets, from the Prionolobus beds of Chideru in the Salt Range. I am not, however, convinced that the generic identity of the two animals is established. The important member of the flora is *Glossopteris*, which seems to be the commonest form, and is accompanied by its stem " Vertebraria ", so that the generic determination may be regarded as certain. It is primarily a Permian form, found in South Africa from the Ecca upward, though it probably does not occur in the Cynognathus zone flora of Aliwal North. In Australia it is abundant from the Lower Marine series up through the Coal Measures of Newcastle, but it probably does not occur in the Narrabeen shales—or higher. Thus it can probably be assumed that *Brachyops* is of Lystrosaurus zone age.

(ii) *Bothriceps australis* Huxley. The type—and only known specimen—was bought by the British Museum in 1848 from a person of whom nothing is known, and was then said to have been found in " Australia ".

(iii) " *Platyceps* " *wilkinsoni* Stephens. There were several described specimens from the well known fish bed of Gosford, New South Wales, which lies in a sandstone member of the Narrabeen shales. One specimen was on loan to the British Museum (Natural History) about 1920–24, when I had a photograph made from it. Its age is relatively well determined ; it is in a formation immediately followed conformably by the Hawkesbury sandstone, from which came the well-preserved fish fauna of Brookvale, described by R. T. Wade in 1935. This fauna is directly comparable with that from Bekker's Kraal in the Cynognathus zone of South Africa, and thus appears to be Lower Triassic.

(iv) "*Bothriceps* " *major* A. S. W. (*non* Owen) comes from a " coal "—actually a torbanite—at Airly, Central Coalfield, New South Wales. This lies in the " Upper Coal Measures ", a formation succeeded by the Narrabeen shales. It is therefore of pre-Triassic age, and may be nearly contemporary with *Brachyops*, or perhaps a little older, in the definitely Permian Cistecephalus zone.

(v) *Batrachosuchus browni* Broom comes from Aliwal North, Cape Province, South Africa, presumably from the Cynognathus zone, Lower Trias.

(vi) *Batrachosuchus watsoni* Haughton comes from an unknown locality certainly in the Cynognathus zone of the Burghersdorp district.

(vii) *Pelorocephalus mendozensis* Cabrera comes from rocks at Potrerillos, Mendoza, Argentina, which on inadequate evidence are regarded as of Upper Middle Triassic age.

Thus in order of age the Brachyopids are :

Rhaetic—*Gerrothorax, Plagiosaurus.*
Upper Trias—*Gerrothorax, Plagiosternum, Plagiosuchus.*
Middle Trias—*Plagiosuchus,* ? *Pelorocephalus.*
Lower Trias—*Batrachosuchus, Platyceps.*
Basal Trias, or Uppermost Permian—*Brachyops.*
Upper Permian (Cistecephalus zone)—"*Bothriceps*" *major.*

Its own structure suggests that *Bothriceps australis* is as early as, or earlier than "*Bothriceps*" *major. Dvinosaurus* from the Cistecephalus zone of Russia is presumably of much the same age as "*Bothriceps*" *major,* and may well have been contemporary with *Bothriceps australis,* or indeed younger.

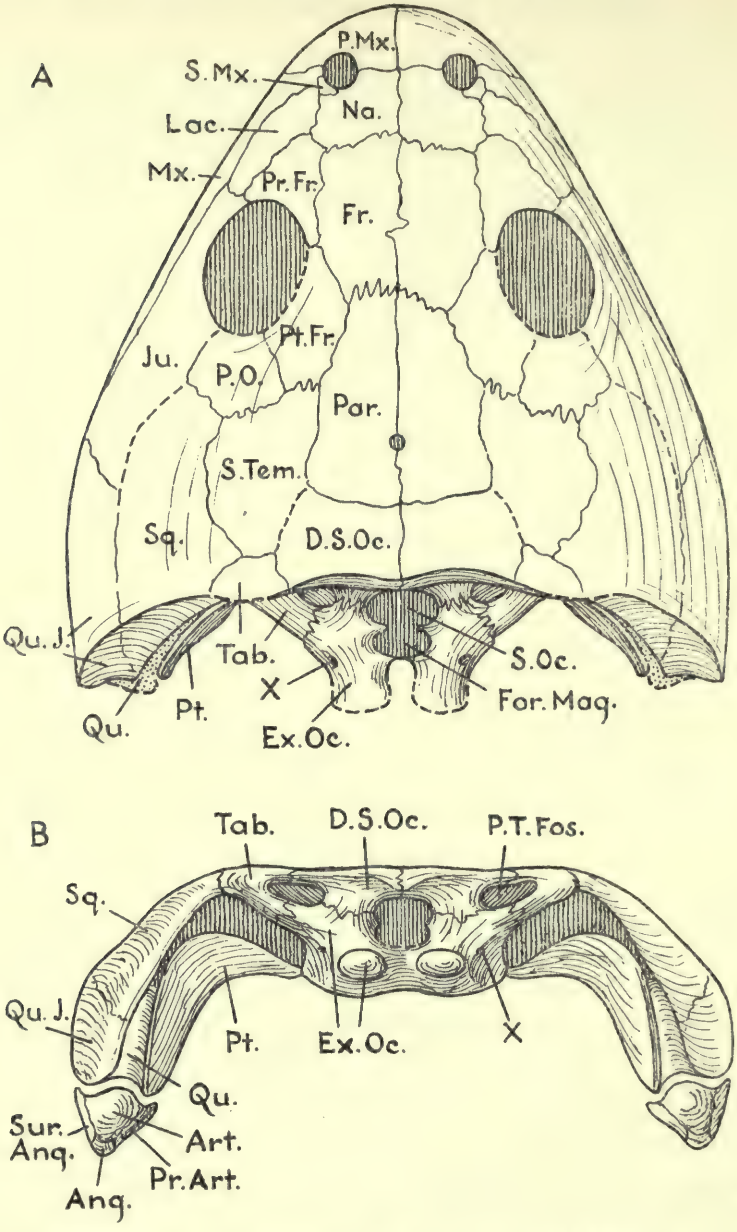
### BOTHRICEPS AUSTRALIS Huxley

The unique type specimen (B.M.N.H., 23110) consists of a skull with the lower jaw tightly closed on it. The whole upper and lateral surface is preserved as a beautiful internal cast, showing the details perfectly, except for some lost regions. To this cast a little actual bone adheres in places and shows, perfectly preserved, the outer surface over small areas, including a lachrymal. The occiput, though damaged, remains as well-preserved bone, and the palate (further developed since 1919) is excellently preserved. Both lower jaws are complete and well shown.

The skull is parabolic in plan and about 15% wider than its length, measured on the skull table. On the left side of the specimen it can very clearly be seen that as far back as the orbit the anterior part of the skull is very much depressed, its ventral border then turning downward so that the skull becomes very deep at the occipital border. The orbits lie almost entirely in front of the mid length, and are comparatively small, so that the face is long for a Brachyopid. The hinder border of the dermal roof is damaged at the lateral end of the tabular, but it seems obvious that there can have been no real otic notch ; indeed there may not have been any embayment at all. The dermosupraoccipitals have a well-marked posterior border on the upper surface, behind which they are produced downward on to the sloping occipital surface by lappets which rest on and end in a suture with the exoccipitals.

The tabulars are short but wide, having a long suture with the supratemporal and the squamosal. They have long occipital flanges passing downward and inward below the large post-temporal fossae to meet the exoccipitals in suture.

The shapes and relations of the main bones of the skull roof can best be understood from Text-figs. 1 and 2. The more important features to which attention should be drawn are : there is a septomaxilla, clearly shown as a small triangular area of bone surrounded by sutures, which is attached to the nasal and lachrymal behind the nostril. The lachrymal is shown on both sides of the skull ; in part the sutures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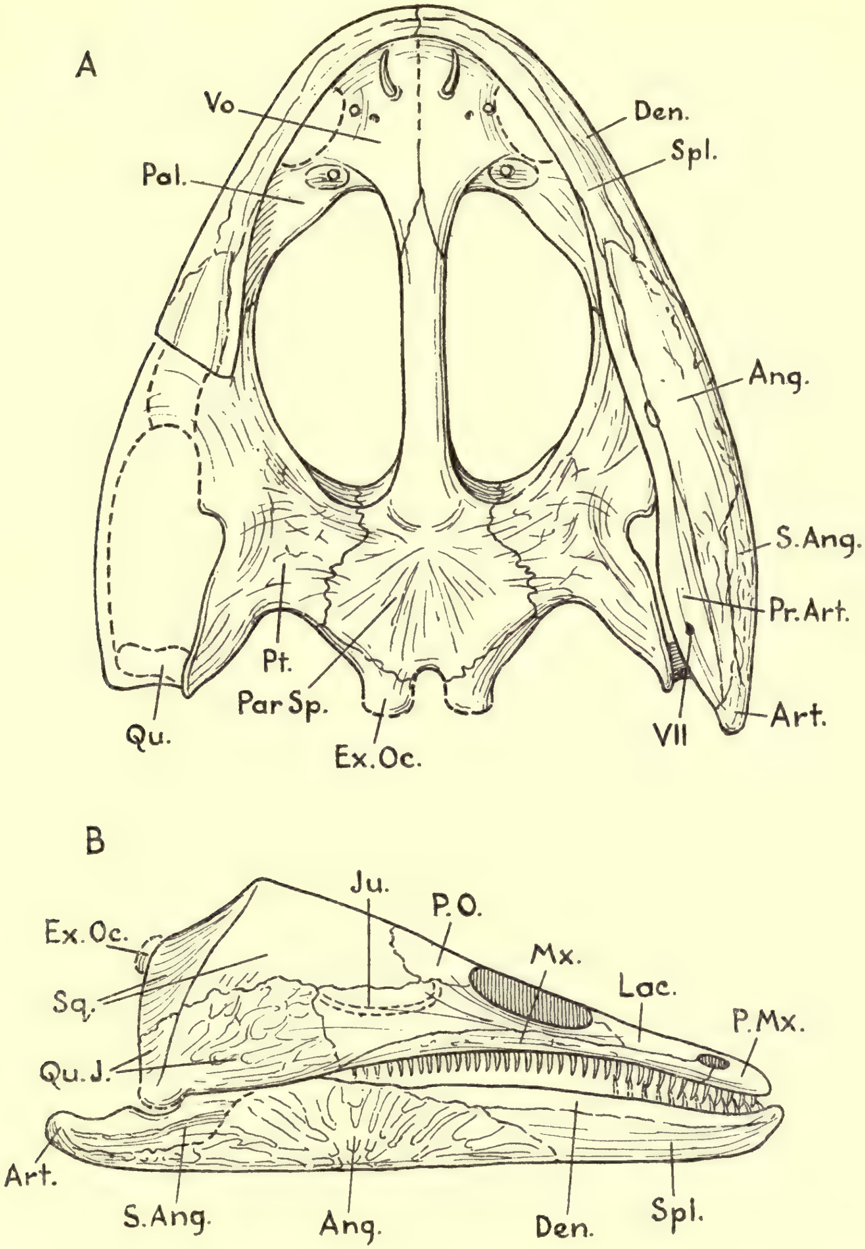
Text-fig. 1.—*Bothriceps australis* Huxley. Type specimen (B.M.N.H., 23110) slightly restored. Natural size. A, Dorsal surface; B, occipital view, with lower jaw in place. The detailed shape of the bones on the skull roof comes nearly entirely from the impression of their under surface, thus the fragments of lateral line grooves shown on the outer surface of the right premaxilla, left lachrymal, and right jugal and squamosal are not represented. *Ang.*, angular; *Art.*, articular; *D.S.Oc.*, dermosupraoccipital; *Ex.Oc.*, exoccipital; *For. Mag.*, foramen magnum; *Fr.*, frontal; *Ju.*, jugal; *Lac.*, lachrymal; *Mx.*, maxilla; *Na.*, nasal; *P.Mx.*, premaxilla; *P.O.*, postorbital; *P.T.Fos.*, posttemporal fossa; *Par.*, parietal; *Pr.Art.*, prearticular; *Pr.Fr.*, prefrontal; *Pt.*, pterygoid; *Pt.Fr.*, postfrontal; *Qu.*, quadrate; *Qu.J.*, quadratojugal; *S.Mx.*, septomaxilla; *S.Oc.*, supraoccipital; *S.Tem.*, supratemporal; *Sq.*, squamosal; *Sur.Ang.*, surangular; *Tab.*, tabular; *X*, tenth cranial nerve foramen.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TEXT-FIG. 2.—*Bothriceps australis* Huxley. Natural size. A, Ventral surface, showing imaginary removal of the hinder part of the right mandible; B, right lateral aspect, showing ornament and lateral line groove where preserved. The lower jaw is restored to its natural position by being lowered so that the quadrate articulated with it regains its original place, and the ornamented outer surface of the angular does not underlie the quadratojugal. The projection of the dentary in front of the premaxilla and the backward direction of its anterior teeth are as in the specimen. Reference letters as before with: *Den.*, dentary; *Pal.*, palatine; *Par.Sp.*, parasphenoid; *Vo.*, vomer; *VII*, foramen for seventh cranial nerve (chorda tympani).

surrounding it are shown on the outer surface of the bone, elsewhere on the mould of the inner surface. The bone does not enter the margin of the nostril, but it is possible that it does form a very small part of the orbital margin. It is entirely surrounded by the maxilla, septomaxilla, nasal, prefrontal and jugal. The pre- and postfrontals meet in suture above the orbit. The jugal forms the whole lateral margin of the orbit, articulating in front with the pre-frontal ? and lachrymal. The large supratemporal meets the postfrontal and postorbital anteriorly, and the dermosupraoccipital and tabular behind. The squamosal is represented mainly by an internal impression, but some bone is preserved. It has a large superficial exposure of ornamented bone ending behind at a definite margin round which the bone turns on to the occipital surface. Here it forms a smooth face standing nearly vertically, and concave on a vertical axis, so that its admesial border is turned backward ending parallel with, but separated by a narrow space from, the hinder border of the quadrate ramus of the pterygoid. This space was obviously occupied by a cartilaginous ridge arising from the visible occipital surface of the quadrate. The quadratojugal is a relatively large bone, lying below and continuing the surface of the squamosal, and extending forward to meet the jugal. That part of it which lies on the outer surface has a normal labyrinthodont ornament, the occipital area being smooth.

The occipital surface is preserved in bone, but is much damaged by weathering and fracture. None the less its structure can easily be made out, and it is represented in Text-fig. 1. The occipital surface slopes backward for a long distance (its own height) behind the ridge on the dermosupraoccipital which marks the hinder border of the skull table. There is no bony basioccipital, but a space which must have been occupied by it exists dorsal to the hinder end of the parasphenoid and between the roots of the exoccipital condyles. The existence of a cartilaginous supraoccipital is shown by the usual shelves on the exoccipitals. The exoccipital condyles are broken off, and the broken surface polished, but they were evidently transversely widened and had a considerable projection backward. The main body of the bone extends upward to meet the occipital lappet of the dermosupraoccipital in a suture, then outward to a suture with the occipital flange of the tabular, forming the lower border of a post-temporal fossa, and evidently sheathing the posterior surface of a cartilaginous paroccipital. The lower part of the bone there passes forward in contact with the upper surface of the lateral border of the parasphenoid to end in a contact with the pterygoid. The exoccipital is perforated by a foramen for the vagus, but it is impossible to be sure whether or not a hypoglossal foramen existed.

The palate, after further preparation by Mr. L. E. Parsons, is well exposed on the left side of the skull, although the adherent lower jaw hides its lateral portions. The parasphenoid has a processus cultriformis with a flat ventral surface which expands into a widened body whose lower surface is also flat, though it is crossed by two shallow grooves which meet in the middle line. It ends in a shallow notch between the pedicels of the exoccipital condyles, the bone is then in contact with the exoccipital by a nearly straight suture extending outward and forward to meet the long one between the parasphenoid and pterygoid. This suture has a rather characteristic sinuous course which can be seen in Text-fig. 2, A. There is no transverse ridge corresponding to that which in *Capitosaurus* represents the pockets for the recti capitis muscles. The pterygoid at its attachment to the parasphenoid is flat, and this horizontal surface extends outward until it rather suddenly turns downward to end at the margin of the subtemporal fossa. The vertical wall so formed extends backward to lie in contact with the admesial surface of the quadrate, so that a thin strip of that bone, and its cartilaginous dorsal continuation, separate it from the corresponding inner flange of the squamosal. It is evident that the lower part of the wall was a sheath covering the inner side of the masticatory muscles. The interpterygoid vacuities are large, their anterior margins lying in the palatines and vomers. There is an alternative pair of large teeth on the palatine, and one very laterally placed on the vomer. The border of the internal nostril is not shown.

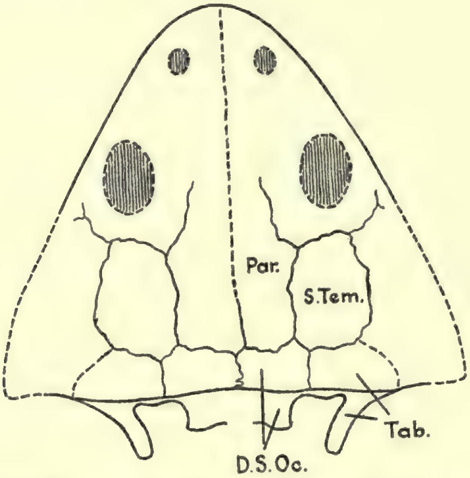
The lower jaw is in postion with the mouth shut. In the specimen the teeth at the front end of the lower jaw lie in front of those in the premaxillae, and much of the maxilla lies mesial of the dentary tooth row. How far this condition is natural I do not know. The lower jaw is shallow and wide. Its ventral surface is straight and there is a large retro-articular process made from the articular, covered laterally by the surangular and angular, and mesially by a prearticular which, just anterior to the articulation with the quadrate, is perforated by a foramen for the chorda tympani. A small Meckelian foramen between the prearticular and angular lies on the inner surface just above the ventral border of the jaw.

## " BOTHRICEPS MAJOR " A. S. W. = TRUCHEOSAURUS **gen. nov.**

The type specimen of *Bothriceps major*, found at Airly in an " oil shale " in the Newcastle Coal Measures of the Central Coalfield of New South Wales, is a large part of a skeleton, one surface being on B.M.N.H., R.3728, whilst the counterpart is in Sydney, New South Wales. The slab in which it is preserved is a bog-head or torbanite, no doubt made largely of the alga *Reinschia*. This material was certainly deposited on the floor of a lake or pool, and the animal must have sunk on to it whilst still nearly (or quite) complete. It has preserved the bones extremely badly, little of them remaining except as a buff coloured film of very small thickness. Thus no preparation is possible.

The specimen in London now consists of two blocks. One contains the head, broken so that the left hinder corner is lost and the occiput is incomplete. The other shows a series of 28 vertebrae and their ribs, no trace of the shoulder girdle remaining. This block extends beyond the preserved part of the vertebral column.

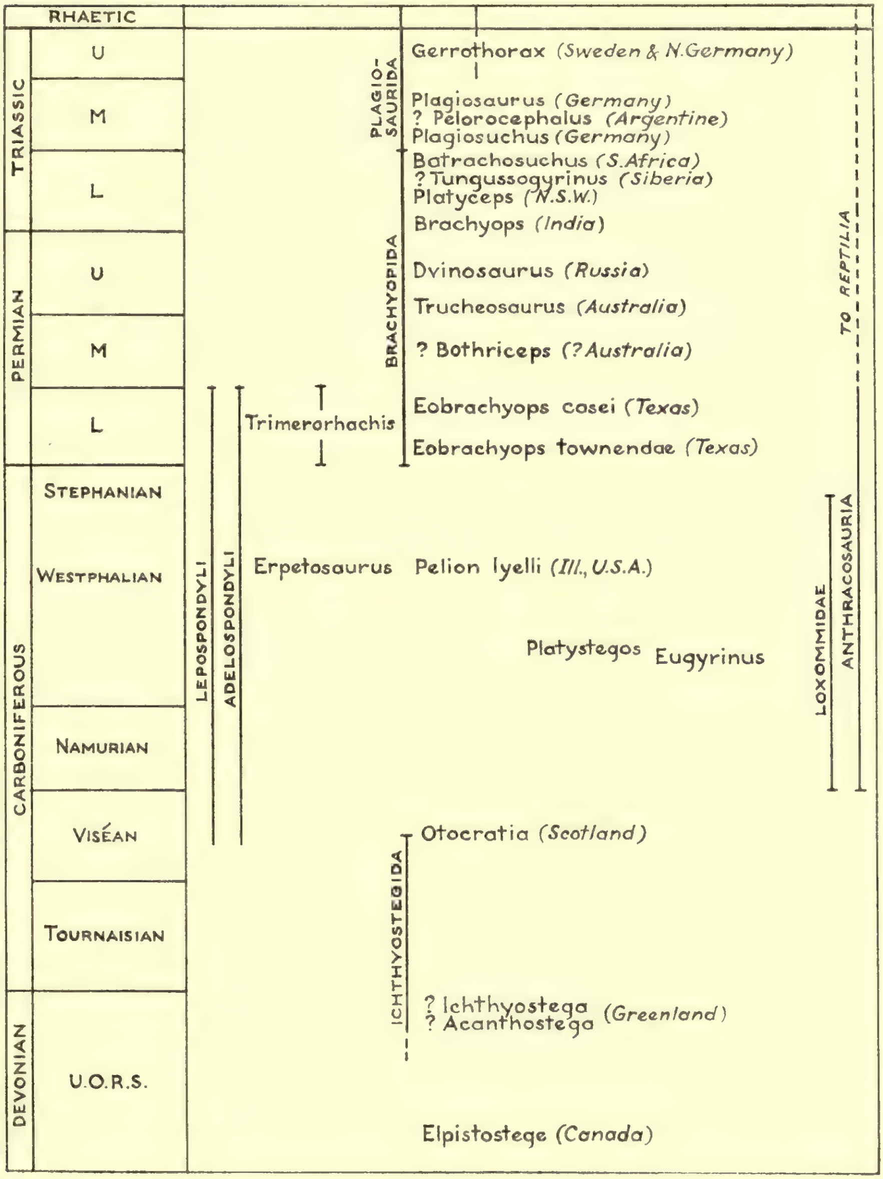
The head and lower jaw are dorsoventrally compressed, and only a faint impression of the upper surface remaining on the slab can be interpreted. The general shape is evident, but it is impossible to be sure of the position of the orbits. The almost straight hinder edge of the dermal roof of the skull is certain, and the lappets of the tabular and dermosupraoccipital which extend backward on to the sloping occiput are well shown. The sutures shown in Text-fig. 3 are derived mainly from the abrupt changes of direction of the ridges which form the ornament of the bones of the skull roof, and these are in all probability a close approximation to the facts. There are no visible traces of lateral line grooves. This skull is evidently that of a Brachyopid : the shortness, great width, presumed anterior position of the orbits, and especially the absence of any otic notch, and straight occipital margin of the skull roof, with the long projection of the occipital surface behind the roof—all facts which are clearly shown and certain—are to be found only in this group of Labyrinthodonts. A small piece of matrix surrounding the occipital process of the tabular and the hinder border of the squamosal on the right side remains. Had the specimen possessed ossified branchial arches some parts of them would have been expected to be preserved in this area, but as there are no such traces visible it is probable that the species was not neotenous. Thus the Brachyopids existed in a typical form in the Upper Permian, presumably in the Cistecephalus zone.



Text-fig. 3.—*Trucheosaurus* ("*Bothriceps*") *major* (A. S. W.) (B.M.N.H., R.3728). Diagram of skull roof. × ⅓. Reference letters as before.

The remainder of the skeleton shows little. The vertebrae are so crushed dorso-ventrally that nothing can be said about them, except that they do not seem to have had the solidity and close approximation of those of the latter Plagiosuchids. The ribs are parallel-sided, little curved, and short—consistent with a broad, dorso-ventrally flattened body. There is evidence of some 28 vertebrae, and their pairs of ribs, preserved; the slab containing the shoulder region is likely to have held 5 more; the series ends before there is any sign of a pelvis and hind legs, which must have lain even further back, although the preserved and inferred part of the backbone is three and a half times as long as the skull. A misplaced fore leg shows a humerus less than a quarter of the skull length in its bony extent, and shorter radius and ulna.

That *Bothriceps major* A. S. W. is a Brachyopid is thus certain, but in the few structures clearly shown in the only known specimen it differs from the type of the genus *Bothriceps*, and indeed from all other known genera of the family. It is thus desirable to place it in a new genus, but the specimen is so poorly preserved that it is quite probable that a well preserved skull of the same species might not be recognizable as such, so that any new genus founded for the specimen would naturally remain without adequate definition. But the specimen is important as showing the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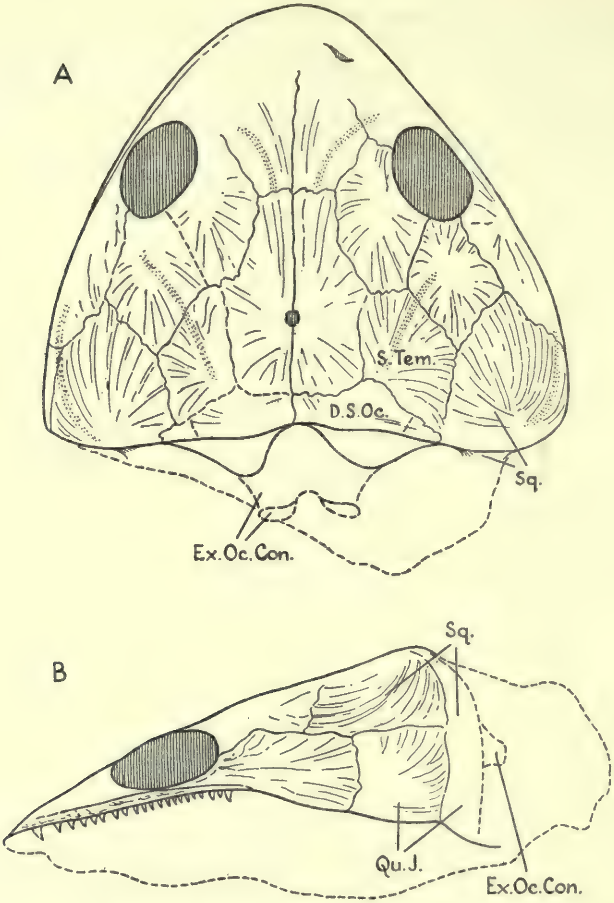
DEVONIAN
U.O.R.S.
PLAGIO-SAURIDA
Gerrothorax (Sweden & N.Germany)
Plagiosaurus (Germany)
? Pelorocephalus (Argentine)
Plagiosuchus (Germany)
BRACHYOPIDA
Batrachosuchus (S.Africa)
? Tungussogyrinus (Siberia)
Platyceps (N.S.W.)
Brachyops (India)
Dvinosaurus (Russia)
Trucheosaurus (Australia)
? Bothriceps (?Australia)
Eobrachyops casei (Texas)
Eobrachyops townendae (Texas)
Trimerorhachis
LEPOSPONDYLI
ADELOSPONDYLI
Erpetosaurus
Pelion lyelli (Ill., U.S.A.)
Platystegos
Eugyrinus
TO REPTILIA
LOXOMMIDAE
ANTHRACOSAURIA
ICHTHYOSTEGIDA
Otocratia (Scotland)
? Ichthyostega
? Acanthostega
(Greenland)
Elpistostege (Canada)

occurrence of a typical Brachyopid at an early horizon, and it must have a generic name for reference, for which I propose *Trucheosaurus* (Gr. *τρυχεα*, rags and tatters).



Text-fig. 4.—*Brachyops laticeps* Owen. Type specimen (B.M.N.H., R.4414). × ½. A, Direct dorsal view; B, lateral view, without reconstruction, dotted outline is that of the matrix. Reference letters as before, with: *Ex.Oc.Con.*, exoccipital condyle.

### Brachyops laticeps Owen

The unique type specimen of *Brachyops laticeps* Owen (B.M.N.H., R.4414) was found at Mángali, Nagpur, Central India, in beds of uncertain correlation but of probable basal Triassic age.

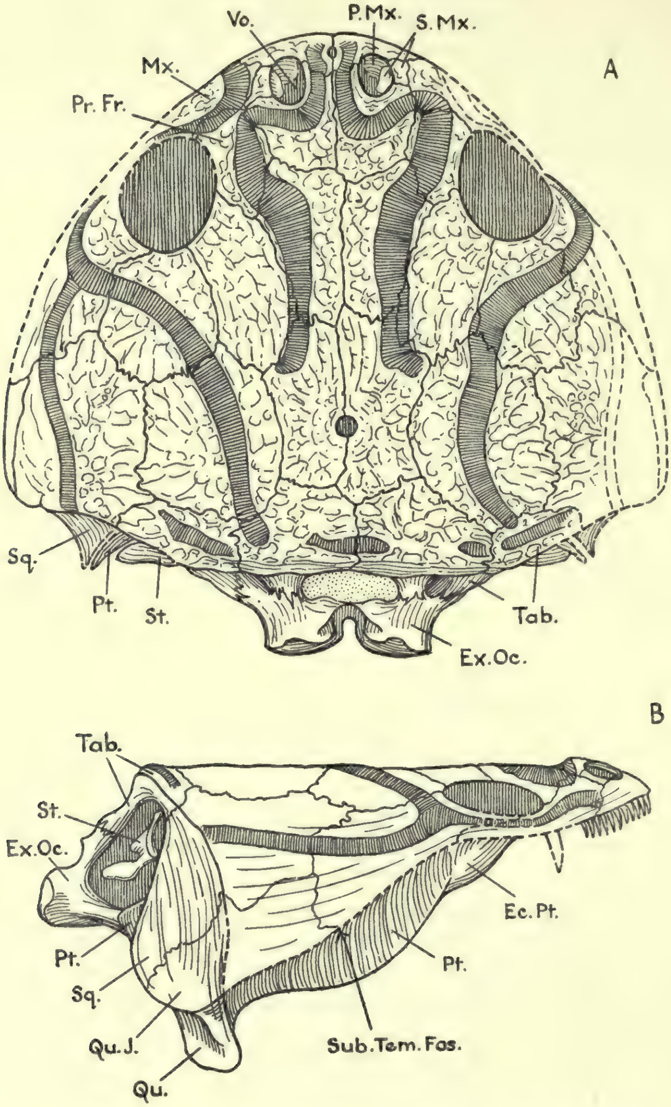
This skull, which lacks a lower jaw, is contained in a curious pink-coloured fine-grained rock, and has very nearly retained its original shape, though the right side is slightly crushed downward and outward. The preservation is unusual and bad. The actual bone seems to have lost its structure; even when seen in transverse section the hinder ramus of the pterygoid is thin and not recognizable under a lens as bone. The superficial ornament of the upper surface is recognizable, though preserved in unnaturally low relief, and imperfectly. The right orbit is well defined, but the position of the pineal foramen is uncertain. The preorbital part of the skull shows its outline, and a possible stretch of the border of the nostril, but is otherwise unintelligible. Sutures are occasionally visible, but must often be inferred from the radiate ornament of the individual bones. Lateral line grooves are sometimes evident. The occiput is present, badly preserved The structure of the dermal skull roof is obvious from Text-fig. 4, A and B, in which the projection of the occiput is certainly fixed, as is the width across the occipital condyles. The characteristic straight occipital border and absence of otic notches are certain, and the specimen shows clearly on both sides the swinging round of the squamosal on to the hinder surface and its termination at a backwardly turned ridge, clearly seen on the left side to be separated by a narrow space of nearly constant width from the hinder edge of the pterygoid seen in section. This space obviously received a cartilaginous ridge on the posterior surface of the quadrate. The lateral line grooves, whose distribution is shown, are relatively narrow, unlike those of *Batrachosuchus*.

In side view (Text-fig. 4, B) it is evident that the hinder part of the maxilla lower (tooth bearing) border is turned a little downward, the lower border of the jugal and quadratojugal continuing its trend. (Dinkel's admirable drawings (Owen, 1855) do not bring this point out clearly, presumably because of some foreshortening by use of a camera lucida.)

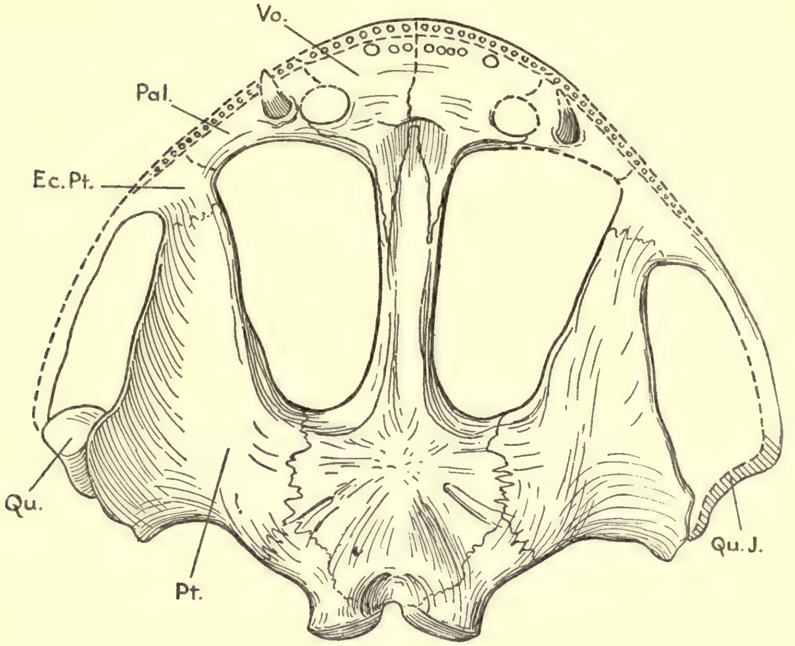
### BATRACHOSUCHUS WATSONI Haughton

The genus *Batrachosuchus* was founded by Broom for *B. browni*, an excellent skull found by Alfred Brown in the Cynognathus beds of the Aliwal North district, Cape Province, South Africa. The only other material is a skull, B.M.N.H., R.3589, from the Seeley collection, which is without any record of origin, but almost certainly came from the Cynognathus zone of the Burghersdorp district. I gave a description of this skull in 1919, and S. H. Haughton subsequently (1925) made it the type of *B. watsoni*. This skull is nearly complete and most perfectly preserved. It is quite undistorted and shows all details of the bones in perfection, but unfortunately the lateral borders of the orbits have been broken away and lost, and the lower parts of the jugals and quadratojugals have been removed, leaving however an impression of the inner surfaces which shows the lower border of the skull with certainty. In my original description I illustrated the skull roof only by a photograph, which was taken at the British Museum in my absence. This was evidently made with a vertical camera, the skull resting on the tip of the quadrate, and on a piece of matrix which supports the premaxillary teeth, when the skull roof lies at an angle of more than 30 degrees with the horizontal. Thus my published photograph is foreshortened, and exaggerates the projection of the occiput and shortness of the skull in relation to its width.

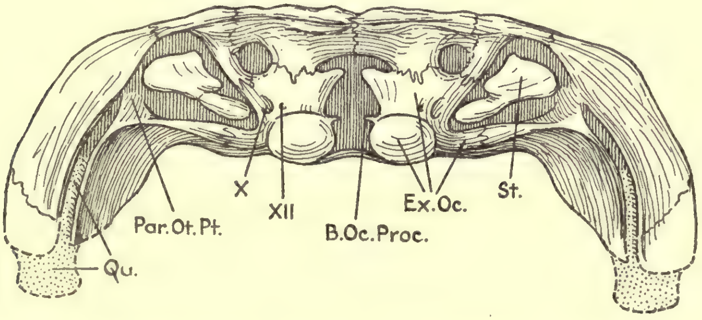
The pattern of the dermal bones of the skull roof is shown in Text-fig. 5 in which it is seen at right angles to its plane, and to the sagittal plane of the skull from a distance


A
Vo.
P.Mx.
S.Mx.
Mx.
Pr. Fr.
Sq.
Pt.
St.
Tab.
Ex.Oc.
B
Tab.
St.
Ex.Oc.
Ec.Pt.
Pt.
Pt.
Sq.
Qu.J.
Qu.
Sub.Tem.Fos.

Text-fig. 5.—*Batrachosuchus watsoni* Haughton. Type specimen (B.M.N.H., R.3589). $\times \frac{4}{9}$. A, Direct view at right angles to dorsal surface, essentially unrestored; B, direct lateral view. The broken line lower border of the temporal region from the hinder end of the maxilla backward follows an impression of the visceral surface of the bones, and is certain. (The quadrate, though shown in solid line, is considerably eroded). Reference letters as before with: *Ec.Pt.*, ectopterygoid; *St.*, stapes; *Sub.Tem.Fos.*, subtemporal fossa.



TEXT-FIG. 6.—*Batrachosuchus watsoni* Haughton. Type specimen (B.M.N.H., R.3589). × ½. The palate, viewed at right angles to the parasphenoid. Reference letters as before. *Qu.J.* is a transverse section of the quadratojugal where it turns inward behind the quadrate to form the characteristic concave surface found only in Brachyopids. It is drawn as it exists in the specimen.



TEXT-FIG. 7.—*Batrachosuchus watsoni* Haughton. Type specimen (B.M.N.H., R.3589). × $\frac{4}{9}$. The occiput seen directly from behind with the upper surface horizontal. Reference letters as before with : *B.Oc.Proc.*, process of exoccipital over the basioccipital cartilage and below the brain cavity ; *Par.Ot.Pt.*, the parotic part of the pterygoid as now exposed, it may reach the skull roof, and extend far in.

of about 100 cm. The only region where the skull roof pattern presents any difficulty is that between the nostril and the orbit. The structure of the premaxillae is obvious; they meet in the middle line, a small opening—perhaps for an interpremaxillary gland—interrupting the suture. They are attached to the anterior ends of the nasals, the two bones together forming the anterior, mesial and hinder borders of the somewhat asymmetrical nostrils. On each side the margin of the nostril is completed by a small bone attached by obvious sutures to the lateral part of the premaxilla in front, and to the lateral part of the nasal behind. These bones are ornamented, each bearing a small knob on its upper surface anteriorly, that on the left having further ornament posteriorly. On the left side I excavated the nostril to its floor, exposing the smooth upper surface of the vomer (separated by a distinct suture from the premaxilla) and found that the bone now under discussion descends from the outer border of the nostril to expand into a small flat sheet resting on the upper surface of the vomer. The posterior end of the vertical part of the bone is notched, and it is clearly a septomaxilla, a simple modification of the ordinary labyrinthodont type.

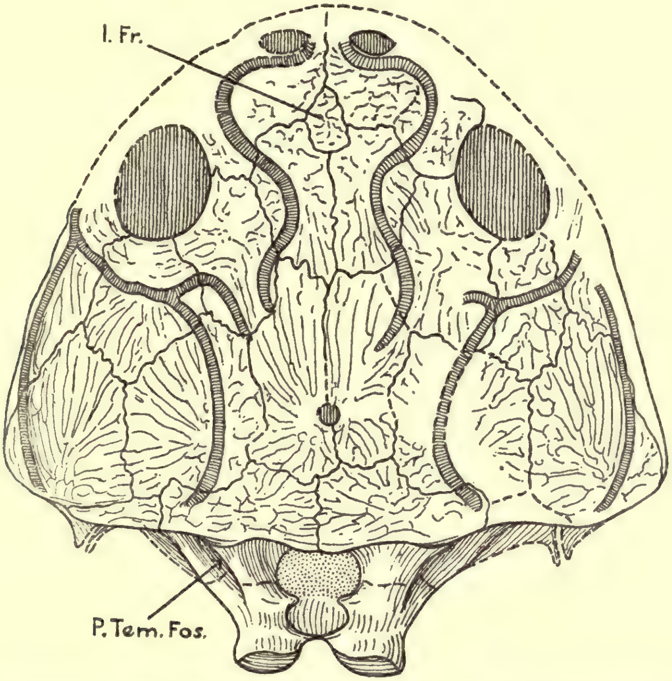
The anterior part of the maxilla is perfectly preserved on each side, its lower border, and the teeth which it bears, being visible on the left side. From here its very highly sculptured surface can be traced upward to an obvious suture with the premaxilla, septomaxilla, nasal and prefrontal. There is thus no sign of a lachrymal; either the bone has fused early in life with the maxilla—which is improbable—or it has vanished, squeezed as it were out of existence by the approximation of the nostril and orbit.

Nothing further in the structure of the skull roof calls for notice here; the whole pattern is determined with certainty. The noticeably anterior position of the quadrates, obscured in my early photograph, is important.

The lateral aspect of the skull (Text-fig. 5, B) brings out its extraordinary shape. The preorbital region is low, there being in fact only a space of some five millimetres in height separating the upper surface of the vomer from the lower surface of the nasal at the hinder margin of the nostril. The depth of the skull at the orbit is much less than the length of that opening, and unless the eye were very small it must have projected far above the skull roof, like that of a frog, and, like the frog's, have been capable of retraction through a special lateral bay in the interpterygoid vacuity. It is remarkable that the orbital margin is not at all everted as is that of *Capitosaurus*. Behind the orbit the skull rapidly deepens until at the quadrate it is remarkably high. The dorsal surface is flat, but it seems evident that there was a break in the direction of the ventral border of the skull roof about at the back of the orbit, the lower margin of the maxilla lying nearly parallel to the skull roof, whilst that of the jugal and quadratojugal lies at an angle of some 40 degrees to it. Thus, as shown in my original figure of the occiput, the quadrate condyle is placed very ventrally, lying far below the ventral surface of the basis cranii.

The posterior border of the skull roof is clearly marked by a ridge which, crossing the flat table, passes outward and downward at the hinder end of the ornamented surface of the squamosal and quadratojugal The smooth hinder surfaces of these bones pass inward and backward round a concave cylindrical surface to end in a free margin, attached to a ridge on the hinder surface of the quadrate bone and its cartilaginous dorsal extension. This ridge is supported on its admesial side by the hinder edge of the pterygoid.

The ornament of the skull roof is of normal labyrinthodont pattern consisting of pits—usually round and separated by low ridges with rounded upper surfaces—but in some regions elongated into short grooves. It is an interesting confirmation of Bystrow's view that the areas with grooved ornament represent regions of relatively large growth in the direction of the grooves, that the grooves on the skull of *B. watsoni* seldom run antero-posteriorly, but often transversely. They are best marked where they run into the suture between the supratemporals and the squamosals—implying a widening of the skull here—and on the postorbital at its suture with the squamosal, which in continuation of them has very small round pits, suggesting that in youth the postorbital was wedged in between the squamosal and supratemporal. Through this normal ornament the lateral line grooves make their way as wide but shallow troughs, usually very broadly V-shaped in section. Their flanks often bear close set, low, transverse ridges. They are very extensively developed, with a normal distribution, though there is a possible transverse groove on the left tabular to which it is difficult to find a parallel.



Text-fig. 8.—*Batrachosuchus browni* Broom. Drawn (with some of the bones put back into place) from a cast of the type skull in Cape Town. × ⅓. *I.Fr.*, interfrontal; *P.Tem.Fos.*, post-temporal fossa.

The occiput was correctly shown in my figure 28 (1919), but further preparation has been made of the left stapes. This is now shown to rise more nearly to the under-surface of the tabular at the admesial end of its upper border, so that the depth of the bone is increased above the notch for a blood vessel, and the ventral surface of the inner end is widened and its anterior part produced downward as a flange which presumably had a sutural attachment to the outer border of the parasphenoid. The pterygoid is shown to have a parotic plate reaching upward toward the cranial roof, on the inner surface of the quadrate from the upper side of the horizontal shelf which projects into the exoccipital and parasphenoid.

### BATRACHOSUCHUS BROWNI Broom

This species is still represented only by the type specimen, which, when Broom described it, was a split slab (? nodule), one side of which showed the visceral aspect of the roof of the skull, the other had been prepared by him to show the palate. Subsequently the South African Museum replaced the skull roof and prepared the ornamented outer surface, which, though a little broken and misplaced, is beautifully preserved ; only the quadratojugals and anterior part of the face are missing. Its structure is shown in Text-fig. 8.

It differs from *B. watsoni* in being proportionately longer and narrower, with the eyes further back, and in the greater projection of the occipital condyles behind the occipital border of the skull roof.

The lateral line grooves have the same general distribution as in *B. watsoni*, but are actually and relatively much narrower and of more U-shaped section. There is a peculiar inwardly and backwardly directed branch of the supratemporal line on the hinder part of the postorbital, absent in *B. watsoni*.

The shapes of the individual bones of the skull roof are essentially the same, though *B. browni* has an interfrontal bone between the frontal and nasals.

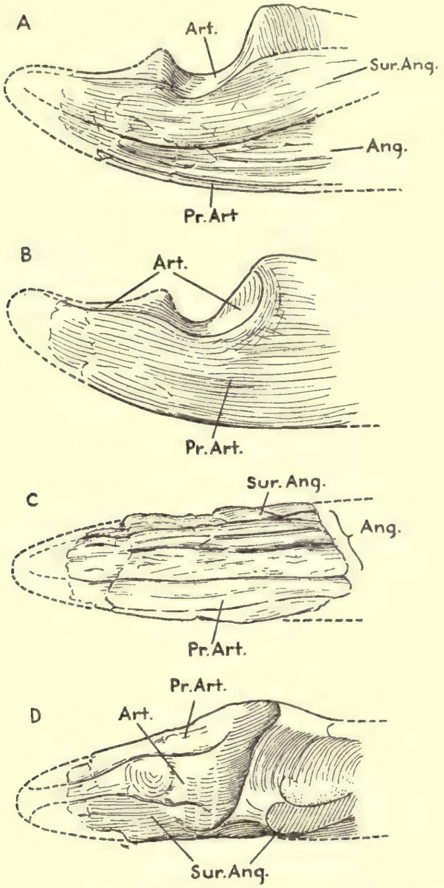
### ? BATRACHOSUCHUS SP.

In 1911 I collected three fragments of labyrinthodont jaw (D.M.S.W., B.126) and an atlas (D.M.S.W., B.140) from a small weathered slope of shale of the Cynognathus zone by the roadside on the farm Luiper Kop between Burghersdorp and Knapdaar Two of the jaw fragments fit together to make the very weathered posterior end of a right mandible, the other is part of the left ramus (including the front half of the articulation) evidently of the same individual ; right and left sides supplement one another and show the structure well.

The essential features (Text-fig. 9) are that the jaw is low, nearly as wide as high at the articulation, with a well formed articular face behind which a long process stretches backward. This has a core of articular, forming a median strip of its upper surface, which is bordered by surangular and prearticular, the angular sheathing a strip of its lower and outer surface. The details of structure differ greatly from those of Capitosaurs, *Benthosuchus*, and the Spitsbergen Trematosaurs described by Tage Nilsson, and there can be no real doubt that the jaw (which much resembles those of

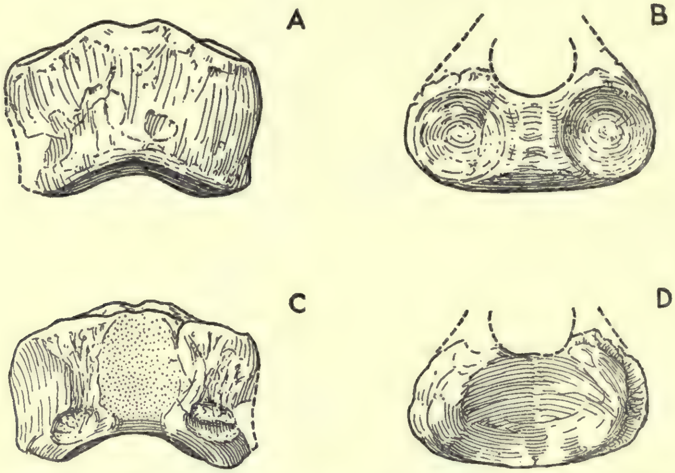
*Bothriceps*, *Pelorocephalus* and *Dvinosaurus*, and is comparable with that of *Eobrachyops*) is that of a Brachyopid. If it be then presumably it belongs to *Batrachosuchus*, which it fits quite well.

Remains of amphibia are so rare in the Cynognathus zone that " association " of labyrinthodont fragments found close together is usually justified, and I therefore describe the atlas found with these jaw fragments as that of *Batrachosuchus*? The atlas (Text-fig. 10), partly covered with a thin haematite film, is much weathered, not completely prepared, and has lost its neural arch. But it is a single bone, only about half as high as it is wide with a laterally concave posterior surface, widening a little anteriorly. The anterior face bears two shallowly spheroidal hollows for articulation with exoccipital condyles which are separated by a rather wide, slightly



Text-fig. 9.—? *Batrachosuchus*. (D.M.S.W., B.126). × ½. Posterior part of a lower jaw, a little restored from fragments of each side. A, Right ramus, outer surface ; B, left ramus, inner surface ; C, right ramus, ventral surface ; D, right ramus, dorsal surface. *Ang.*, angular ; *Art.*, articular ; *Pr.Art.*, prearticular ; *Sur.Ang.*, surangular.

hollowed and pitted surface. The floor of the cavity for the spinal cord is wide and somewhat depressed over its length ; the roots of the neural arch are, so far as can be judged, extremely slender. The lower surface of the bone is pitted by irregular, often longitudinal depressions. The specimen measures 4·8 cm. across the condylar depressions. The condyles in *B. browni* are 6·0 cm. across. In *B. watsoni* the corresponding width is 5·0 cm., only a few millimetres greater than that of the atlas, and the same depth. The only important recognizable feature is the absence of any indication that the atlas was ever more than a single bone.



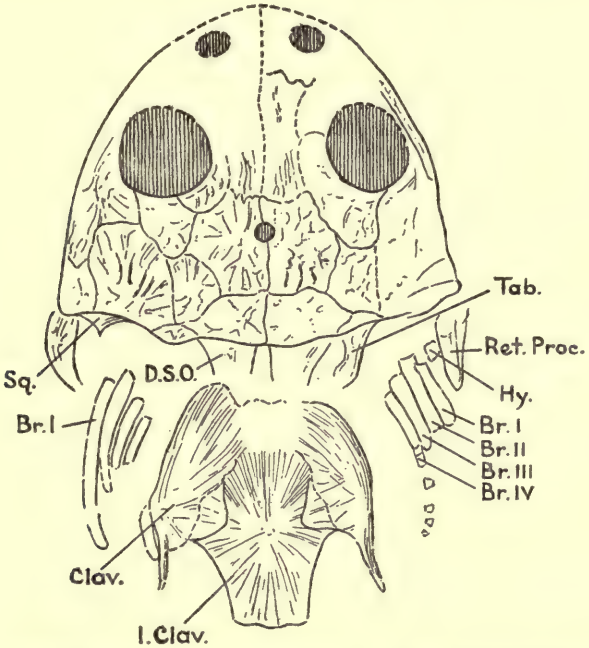
TEXT-FIG. 10.— ? *Batrachosuchus.* (D.M.S.W., B.140). × $\frac{2}{3}$. Atlas associated with the original of Text-fig. 9. A, From below ; B, from in front ; C, from above ; D, from behind.

### PELOROCEPHALUS MENDOZENSIS Cabrera

The specimen, a skeleton, was found as a weathered impression to which films of bone adhered, showing the palate and misplaced lower jaw. The palate, as Cabrera rightly recognized, is extremely like that of *Batrachosuchus*, agreeing in general proportions very closely with *B. browni* though (very probably owing to the imperfect preservation) the subtemporal fossa is rather wide. The condyles agree, and the suture bounding the parasphenoid is shown sufficiently to make it evident that the exoccipital met the pterygoid in a long suture. The lower jaw shows an anterior border to the articular facet exactly similar to that in the jaw referred above to *Batrachosuchus*, and the remains of a similar long retroarticular process. The specimen is preserved in Buenos Aires.

### " PLATYCEPS " WILKINSONI Stephens

The following account is based on an enlarged photograph of the type specimen, which I actually handled about 30 years ago, (Pl. 39 and Text-fig. 11). The specimen, which extends backward to show some 25 body segments, is seen from above as dark grey crushed bone on a grey-yellow, fine-grained sandy matrix. The lower jaws are in position and the head, shown from above, is widened by being flattened almost into a plane. The skull is widest across the quadrate condyles and is semi-elliptical. The occipital border is straight and lies behind the quadrates, there being some rounding of the hinder edge of the tabular to enable it to pass directly into the hinder border of the ornamented outer surface of the squamosal. Squamosal and quadratojugal pass inward, behind the quadrate, and then backward. The jugal is extremely shallow lateral to the large orbit, and the shallow maxilla stretches backward below it. The orbits are widely separated, of considerable size, but leave a relatively large preorbital face. The tabulars and dermosupraoccipitals bear powerful occipital flanges which pass backward and inward, showing that the condyles must have been placed far back, though it is evident that the dermal processes have been flattened out into the plane of the skull top and the extent of their projection back thus exaggerated. The retroarticular part of each jaw ramus is visible as a long projection.



TEXT-FIG. 11.—"*Platyceps*" *wilkinsoni* Stephens. × 1⅔. Tracing of the skull, branchial arch skeleton and dermal shoulder girdle, made from an enlarged photograph of a specimen (the type) from Gosford, New South Wales, now in Sydney. (Compare with Plate 39). *Br.I–IV*, branchial arch skeletons I–IV; *Clav.*, clavicle; *D.S.O.*, dermosupraoccipital; *Hy.*, hyoid arch skeleton; *I.Clav.*, interclavicle; *Ret.Proc.*, retroarticular process of the lower jaw; *Sq.*, squamosal; *Tab.*, tabular occipital process.

The most striking quality is, however, the presence of long bony ceratobranchials. The ceratohyal is, perhaps, visible on each side of the head as an obscure stain mesial to the long retroarticular process, but four ceratobranchials are clearly shown on each side between this element and the outline of the body as suggested by the clavicle. Each ceratobranchial is a bony rod lying close pressed against its fellows, the anterior ends of the rods seem to lie along a line placed obliquely, its outer end further forward than its mesial point. The chief bones in all the arches are of much the same length, but it is evident on the left side that the first ceratobranchial is greatly extended by some structure—presumably cartilage—for a very long distance, whilst on the right side the last ceratobranchial has three or even more independent rings of bone surrounding its distal end, and there is a suggestion of a very extensive spread of soft structures beyond them.

The vertebral column is represented by paired series of structureless bony masses. These seem to be in general paired ossifications in the neural arches, with slight suggestions of other paired ventral bones. The ribs are short, nearly straight bones, widening proximally in a manner which suggests that they may have had double cartilaginous heads, but actually ending as bone some distance lateral of the vertebrae. The distal ends of the ribs sometimes widen, possibly as a result of crushing of a very thin bony cylinder. The first three vertebrae seem to be somewhat more massively ossified than those further back, but curiously there seem to be no ossifications in the exoccipital condyles.

The dermal shoulder girdle is well shown from above, the structure of its lower surface " printing through ". The interclavicle is large, two-thirds as long as the skull table, and its anterior end seems to have been almost semicircular, the widest point being about at mid length. From here its lateral borders pass inward and backward to end abruptly at a nearly straight transverse posterior border. The clavicles have a long overlap on the ventral surface of the antero-lateral parts of the interclavicle, and probably just meet at its anterior end. Their ventral parts are expanded, the dorsal process apparently turning a little backward and being capped by a cleithrum.

The scanty ossification of the vertebral column and the apparent lack of ossification in the exoccipitals suggest that *Platyceps* is very young, as indeed its very small size in comparison with other Brachyopids makes probable. The well ossified ceratobranchia thus imply that the animal retained its external gills into adult life, and was neotenous, as seems to have been the case in the " Plagiosaurid " *Gerrothorax*, where Nilsson (1945) has recorded the existence of ossified ceratobranchials in an obviously adult animal.

## " PLAGIOSAURIDS "

### Description of Material

The genus *Plagiosternum*, established by E. Fraas (1889) for fragments from the Upper Muschelkalk of Crailsheim, has had other specimens referred to it. But the skull is still represented by fragments whose areas do not overlap, so that all that can be said about it is that it may well have resembled those of *Plagiosaurus* and *Gerro-*

*thorax.* The skull described by Fraas (1913) as " *Plagiosternum* " *pulcherrimum* (now referred to the genus *Gerrothorax*) is the only one belonging to the group which is undistorted and really well preserved, but unfortunately the hinder surface of the quadratojugal and quadrate is broken off on the right side and completely missing on the left, and sutures are difficult to trace on the very richly ornamented outer surface. Von Huene (1922) was the first to attempt to do so. Tage Nilsson (1937) has produced another version which for the postorbital part agrees reasonably with von Huene's paper, but differs absolutely for the more anterior regions. Nilsson's account of a Swedish specimen, *Gerrothorax rhaeticus,* includes a description of a strip of the hinder part of the dorsal surface of a skull whose dorso-ventrally compressed occiput is also shown, and inspection of the material shows that his excellent figures make the structure evident. Thus we have evidence in support of Nilsson's reading of the difficult skull now in Stuttgart.

A fragment of the right hinder corner of a skull from Halberstadt, the type of Jaekel's *Plagiosaurus depressus,* is illustrated by Nilsson in an excellent photograph, and the structure of its dorsal surface is evident. It is differentiated from all others by the meeting of the dermosupraoccipital and postfrontal (!) so that the parietal does not touch the supratemporal.

The only other described genus is *Plagiosuchus* von Huene (1922). This is represented by a skull whose palate is largely shown, two misplaced lower jaws, an atlas, some ribs, a scapulocoracoid and clavicles and interclavicle, in articulation but incomplete posteriorly. There are no ways in which this specimen can be compared in detail with other Plagiosaurs, but it is important because its lower jaw has an immense retroarticular process, similar to, though proportionally longer than that which I have described above as *Batrachosuchus.* There is also an atlas, a single bone again much like the one I have referred to *Batrachosuchus.*

## Points of Agreement with Older Brachyopids

Thus the Plagiosaur skull is reasonably well known : it agrees with that of the older Brachyopids in such important characters as :

(1) The way in which, as shown in *Gerrothorax rhaeticus, G. pulcherrimus* and *Plagiosaurus depressus,* the pretympanic flange of the squamosal wraps round the outer side of the quadrate and forms a laterally concave face on the occipital surface, ending, as far as one can judge from the somewhat damaged material, in a ridge which faces a similar border of the pterygoid, the nature of the quadrate not being clearly shown.

(2) The up-turning of the lateral wings of the pterygoids from the subtemporal fossae, so that the palate forms a broad ∩-shaped arch (seen in *G. pulcherrimus,* less well in *G. rhaeticus* and *Plagiosternum granulosum*).

(3) The fact that the occipital condyles lie far behind the dermosupraoccipital.

(4) The absence of an otic notch.

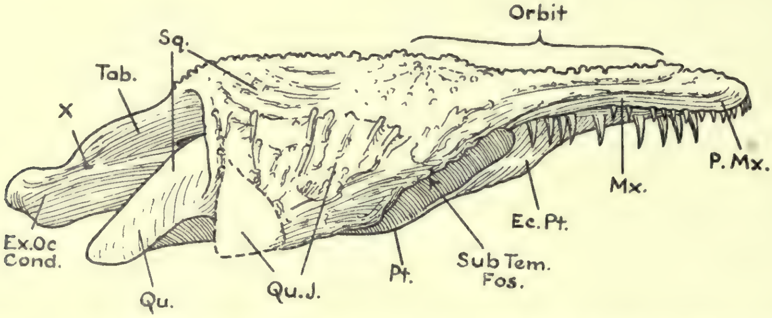
(5) The broad parabolic outline.

(6) The existence of a very large retroarticular process of the lower jaw.

(7) The extreme shallowness of the anterior part of the skull to the hinder end of the maxilla, and the deepening seen in side view, from a point behind the orbit to the quadrate condyle (cf. Text-fig. 12).

The differences in the pattern of the dermal bones of the skull roof, which distinguish the various genera, are obviously due to " improvisations " to enable a series of bones growing outward from centres more or less fixed to fill a steadily contracting area. Even in *Batrachosuchus* this difficulty is seen in the preorbital surface ; in the Plagiosaurs it spreads to the temporal region.

Thus the close relationship between the Upper Permian and Lower Triassic typical Brachyopids and the Middle and Upper Triassic Plagiosaurs is obvious, depending on special detailed common peculiarities not known in any other contemporary Labyrinthodonts.



TEXT-FIG. 12.—*Gerrothorax pulcherrimus* (Fraas). Drawn from a cast in the Museum of Zoology, Cambridge. × ⅗ approx. Lateral view of the skull based on a photograph taken at a distance of some 12 ft., and then enlarged : it is thus very nearly a parallel projection. *Ec.Pt.*, ectopterygoid; *Ex.Oc.Cond.*, exoccipital condyle ; *Mx.*, maxilla ; *P.Mx.*, premaxilla ; *Pt.*, pterygoid ; *Qu.*, quadrate ; *Qu.J.*, quadratojugal ; *Sq.*, squamosal ; *Sub.Tem.Fos.*, arrow directed into the subtemporal fossa ; *Tab.*, tabular ; *X*, tenth cranial nerve foramen.

## DVINOSAURUS COMPARED WITH OLDER BRACHYOPIDS

In 1919 I suggested that the then undescribed *Dvinosaurus* from the Russian Upper Permian was a possible ancestor of the Brachyopids, pointing out (1926 : 199) the existence of bony branchial arches and suggesting that the animal was neotenous. In 1936 a description of *Dvinosaurus* by P. P. Sushkin was published posthumously ; this is still of great value, even though in 1938 Bystrow gave us a beautifully illustrated account and discussion of the animal. Sushkin accepted the view that *Dvinosaurus* and *Batrachosuchus* are close relatives, though demurring—obviously rightly—that, as *Dvinosaurus* is neotenous, it cannot well be an actual ancestor of the other form. He was at that time the only man who had examined both animals, and he added to the set of resemblances I had set out the remarkable similarity between the stapes of the two animals, a matter of importance, for the massive bone differs greatly from those of all other Labyrinthodonts.

Bystrow agrees that in general appearance the skull of *Dvinosaurus* resembles the Brachyopids, but finds (pp. 271, 272) a series of differences which are :

(1) *Batrachosuchus*, though very large, lacks ossified basioccipital and supraoccipital.

(2) In *Batrachosuchus* the parasphenoid and the pterygoids are united by a strongly toothed suture, whereas in *Dvinosaurus* this arrangement is lacking. If there be an attachment between these bones in *Dvinosaurus* it has no resemblance to the long " sutura paraspheno-pterygoidea " of *Batrachosuchus.*

(3) Other matters in which *Batrachosuchus* differs still more from *Dvinosaurus* are the reduction of the paroccipital, the loss of any trace of the intertemporal, the proportionately short palatal ramus of the pterygoid, and the passage of the sulcus jugalis (of the lateral line) along the squamoso-quadratojugal suture.

Most of these differences are the results of evolutionary change of characteristically labyrinthodont type, since :—

(1) All early (Lower Permian) Labyrinthodonts have a well-developed basioccipital, some few a supraoccipital, bone. All Upper Triassic Labyrinthodonts lack both bones.

(2) Several Lower Permian, and nearly all Upper Carboniferous, Labyrinthodonts have a movable articulation of the pterygoid on the basipterygoid process. All Triassic Labyrinthodonts have a long sutural attachment of the pterygoid to the parasphenoid.

(3) All Lower Permian Labyrinthodonts (except *Eobrachyops*) have an ossified paroccipital—in part visible from behind—but no Upper Triassic form retains that condition, the paroccipital ceasing to be ossified and being concealed from view by a meeting of the exoccipital and tabular. An intertemporal bone exists in Seymouriamorphs of all ages, and in many early Labyrinthodonts—for example, it is present in *Loxomma* but has been lost in all other Loxommids. Amongst Rhachitomi an intertemporal is present in the so-called Edopsids (most of which are of Pennsylvanian age) and in Romer's Trimerorhachoidea (mostly Carboniferous, with some early Permian descendants). All other Rhachitomi and Stereospondyli lack an intertemporal, obviously by loss. Thus its occurrence in *Dvinosaurus* is merely the retention of a primitive character.

By a comparison between all then-known Lower Permian and all Triassic Labyrinthodonts I showed in 1919 that a great enlargement of the interpterygoid vacuities was a characteristic change found in that group as it is traced from its beginning to its end. Thus the reduction in the length of the palatal ramus of the pterygoid in *Batrachosuchus* as compared with *Dvinosaurus* is exactly what would be expected.

The passage of the sulcus jugalis along the squamoso-quadratojugal suture in *Batrachosuchus* does not exist ; Bystrow was unfortunately misled by my published photograph.

The only other difference is that in *Dvinosaurus* the interclavicle has a long narrow posterior extension and a median incision as a long narrow slit anteriorly, whilst in " *Platyceps* " the interclavicle has a wide posterior end terminating in a gently rounded but essentially transverse border, and no indications of an anterior median slit. The clavicles of *Dvinosaurus* nearly approach one another but are narrow, whilst those of "*Platyceps*", also not in contact with one another, are greatly widened ventrally. There is thus a real difference between *Dvinosaurus* and the later forms.

But *Dvinosaurus* is neotenic: it retains a larval condition physiologically and structurally. It is true that "*Platyceps*" is larval and probably neotenic, as is *Gerrothorax*. But it is probable that the extent to which larval qualities were lost in neotenic Labyrinthodonts could vary, for metamorphosis was obviously a long process in Labyrinthodonts, for example in *Archegosaurus*, where an animal with a skull length of 7·0 cm. may still retain the denticles guarding the inner openings of the branchial clefts. Narrow lower ends to the clavicles are found in *Eryops* and in Branchiosaurs, and may well be a persistent larval feature.

Romer (1947 : 125) accepts Bystrow's view, and elaborates a comparison with *Trimerorhachis* and *Saurerpeton*. But Sushkin had, with a true instinct, recognized that in *Dvinosaurus* . . . " there is a well differentiated processus internus of the pterygoid, tapering admesially; its posterior edge being thickened and bearing a facet for the articulation with the parasphenoid; the articular surfaces of the pterygoid and parasphenoid fit completely and there is no ground for supposing that there existed also a junction of the pterygoid with a true processus of the chondrocranium which may not have been preserved in the fossil condition ". He recognized a real resemblance to *Trimerorhachis* in this matter. It is evident that the condition is unusual, the original basipterygoid process having vanished in association with a great thinning of the basisphenoid, a new articulation between membrane bones having taken its place. I can see no reason why the parasphenoid and pterygoid so brought into apposition should not later gain a sutural connection, as they did in the development of *Eryops* from an *Edops*-like ancestor where, however, the basisphenoid core of the process remains (even long after the sutural attachment of the two membrane bones has spread into a long flat sheet) as the cartilaginous infilling of the " conical recess ". Thus this character is no evidence against a close association between *Dvinosaurus* and the Brachyopids.

I would add to the features in which *Dvinosaurus* resembles the Brachyopids the fact, shown in the two side views of the skull and lower jaw published by Sushkin (1936 : 60, fig. 4) and Watson (1951 : 102, fig. 42), that the face is very shallow, the temporal region relatively deep.

## EOBRACHYOPS TOWNENDAE **gen. et sp. nov.**

### Description of Material and Manner of Fossilization

Some twenty-five years ago I found, in the mass of unattractive, unregistered Texan Permian material belonging to the Cope collection in the American Museum of Natural History, a small Labyrinthodont skull almost entirely covered by a most unpromising matrix. This was mainly a very hard, dark red, cemented mudstone, partly represented by spheroidal nodules and for the rest by the light green matrix in which bone structure is usually destroyed. This specimen I prepared with a hammer and needle-pointed chisels in odd hours during the early part of the late war when I was fully engaged in government work. The preparation is satisfactory, such matters as the surface ornament and sutures on the outer surface being perfectly shown. But the specimen has been damaged, and it is necessary to explain its condition in some detail to justify the restored drawings which I now publish, and to bring out its eventful history, which has a bearing on the mode of deposit of the rocks in which it was buried.

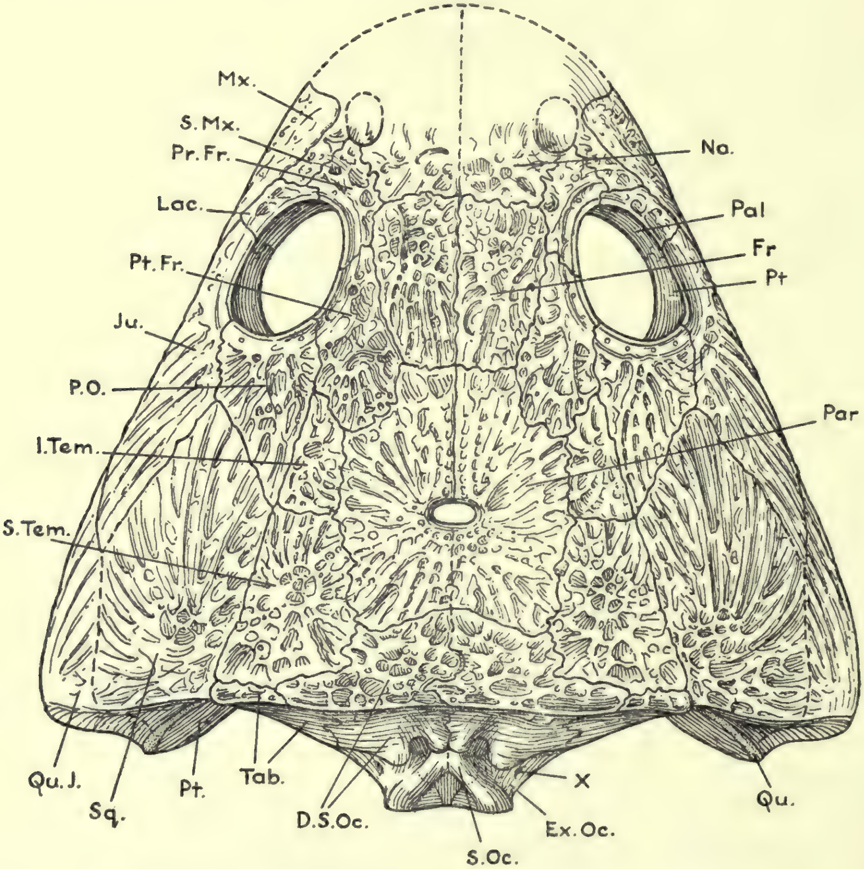
The skull, very shallow in front, is deep in the occipital region. The extreme end of the nose, and part of the anterior surroundings of the left orbit, had been broken off and lost before collection, and the right quadrate region is weathered away. The animal after death was disturbed ; the left squamosal turned outward into the plane of the upper surface, the left pterygoid disarticulated and carried over to the right side of the palate. It now rests on the ventral surface of the right clavicle, which has moved forward so that its dorsal ramus passes up through the right interpterygoid vacuity to the roof of the skull. The left ramus of the lower jaw is misplaced so that its inner surface faces upward, lying below, and separated by some 5–10 mm. from, the visceral surface of the left squamosal. The anterior part of the jaw was not collected. Below this jaw lies the interclavicle with its anterior end forward. On the ventral side of this bone lie a number of vertebral elements, whilst the ventral surface of the right clavicle is underlain by some ribs and a number of dermal scales, of which others are to be found elsewhere. Such disturbance seems to me of a kind which might have been brought about by pulls given by small animals at a time when a good deal of the skin and other soft parts were still present, and the whole appearance is more consistent with a drying carcass than with one under water.

After these displacements the skull was fractured, two cracks crossing the table from side to side, the central strip so separated being depressed 2–3 mm. below its surroundings. At the same time the upper end of the dorsal ramus of the clavicle was forced through a parietal, the fragments so formed standing up round its tip like a tent, and the exoccipitals were fractured and forced up relative to the descending flanges of the dermosupraoccipitals. It is obvious that these fractures can only have been made by pressure exerted by a heavy soft body into which the tent of parietal fragments, still held together by skin, could have been forced. And the only such structure I can think of is the foot of a large animal : and an animal foot could only exert sufficient pressure in air.

Despite this damage it is possible to make reconstructions which must be nearly accurate, as the right squamosal is in its natural position, though the quadratojugal has been forced upward within it and has lost its lower margin. The orbital part of the skull is extremely flattened in the actual specimen, but seems to retain very nearly its original shape. The extreme depth of the cheek at the quadrate was suggested by continuing the anterior part of the border of the quadratojugal backward, and estimating the place of origin of the surface ornament of that bone from the radial arrangement of its surviving parts. The point so determined is confirmed because it enables a drawing of the lower jaw (previously made in what appeared to be a natural position) to have an obviously natural occlusion when placed in articulation with the inferred quadrate condyle. The reconstructions were made by Miss J. Townend after we had agreed on all matters of detail.

## SKULL ROOF

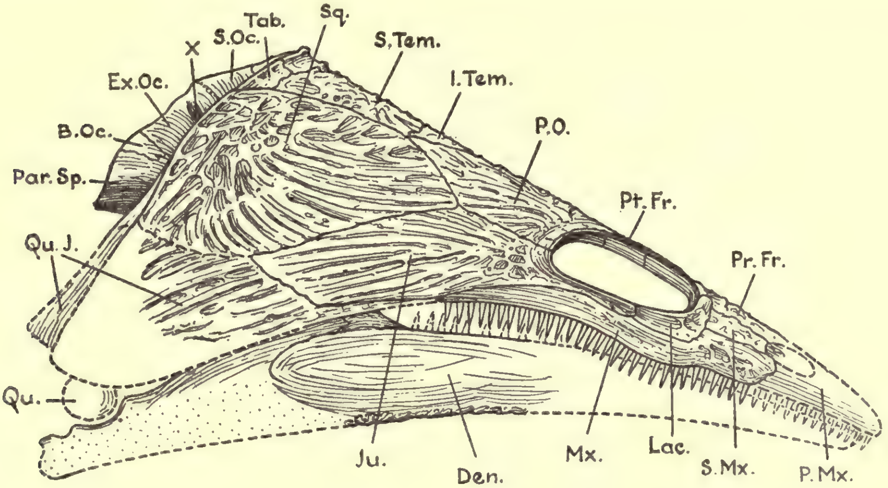
The remarkable features of the skull roof are the small size, wide separation, and very anterior position of the orbits, and the absence of an otic notch. All the bones of a normal Labyrinthodont skull roof are present, those which build up the " table " covering a very unusually large part of the whole area.



**Text-fig.** 13.—*Eobrachyops townendae* gen. et sp. nov. Reconstruction of the type specimen (A.M.N.H. 2455). $\times 1\frac{1}{3}$. Dorsal aspect of the skull, viewed at right angles to its upper surface. *D.S.Oc.*, dermosupraoccipital ; *Ex.Oc.*, exoccipital ; *Fr.*, frontal ; *I.Tem.*, intertemporal ; *Ju.*, jugal ; *Lac.*, lachrymal ; *Mx.*, maxilla ; *Na.*, nasal ; *P.O.*, postorbital ; *Pal.*, palatine ; *Par.*, parietal ; *Pr.Fr.*, prefrontal ; *Pt.*, pterygoid ; *Pt.Fr.*, postfrontal ; *Qu.*, quadrate ; *Qu.J.*, quadratojugal ; *S.Mx.*, septomaxilla ; *S.Oc.*, supraoccipital ; *S.Tem.*, supratemporal ; *Sq.*, squamosal ; *Tab.*, tabular ; *X*, tenth cranial nerve foramen.

The large parietals surround a transversely widened pineal foramen, meet the frontals anteriorly, and are bordered laterally by the postfrontals, intertemporals and supratemporals. Posteriorly they are attached to the dermosupraoccipitals which stretch outwards behind the supratemporals to sutures with the small tabulars. The presence and relations of the intertemporal are quite certainly shown ; it lies between the parietal, postfrontal, postorbital and supratemporal—the position it holds in all those Labyrinthodonts in which its occurrence has been described.

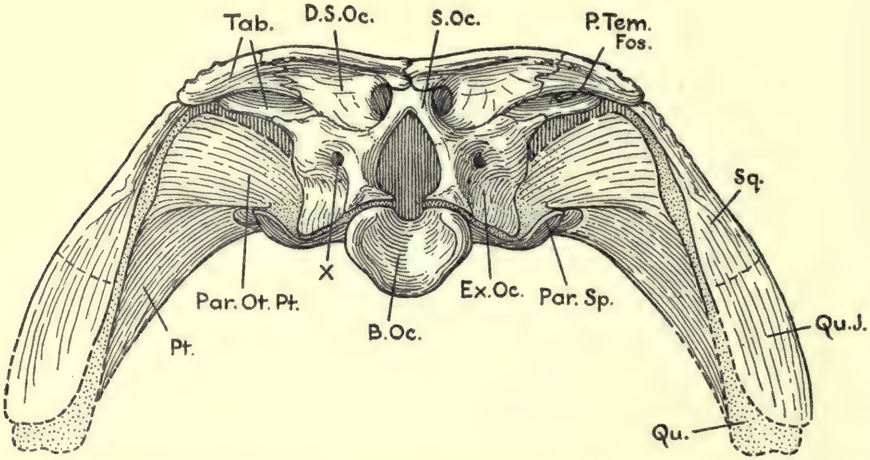
The squamosal is a remarkable bone, standing nearly vertically on the side of the skull, articulating above by a long straight suture with the supratemporal and tabular with its anterior end wedged in between the long postorbital and the jugal, with which it has a very long suture. The upper part of the hinder border of the bone is narrow and is separated by a now empty space from the upper part of the posterior margin of the quadrate ramus of the pterygoid. Ventrally the hinder edge of the squamosal is turned (over a rounded surface) abruptly inward nearly at right angles to its outer surface and extends inwards toward, though it does not come into contact with, the lower part of the hinder border of the pterygoid. The inner border of this part of the squamosal is turned backward, no doubt applied to a narrow ridge of the cartilaginous quadrate whose other surface was coated by the pterygoid.



TEXT-FIG. 14.—*Eobrachyops townendae.* × 1⅓. Lateral aspect of the skull and lower jaw. Reference letters as before with : *B.Oc.*, basioccipital ; *Den.*, dentary ; *P.Mx.*, premaxilla.

The arrangement of the bones surrounding the orbit is shown with certainty. There is a large postfrontal, articulating with the postorbital, intertemporal, parietal and frontal bones, which ends anteriorly at a suture with the prefrontal. The prefrontal is attached by its inner border to the frontal and nasal, and most unusually extends forward to form part of the border of the nostril. The posterior part of the lateral border is in contact with the lachrymal, the remainder with a bone whose nature has to be discussed. This bone is excluded from the orbital margin, its posterior end being attached to that upstanding process of the lachrymal which reaches the prefrontal. From here forward to the nostril the bone is held between the prefrontal and the maxilla, its anterior border forming a good deal of the margin of the nostril. Except for a very remote possibility that the lachrymal may only be a broken anterior part of the jugal, the neighbours of this puzzling bone are certainly determined, and the only homologue which can be found for it is the septomaxilla, which sometimes has a superficial exposure.

The lachrymal is a small bone forming the anterior and lower corner of the orbital border. It is a little misplaced, but a notch bounded by the prefrontal and septomaxilla shows its original position, and the mode by which it articulates with the upper surface of the maxilla is obvious. The bone turns inward to form a wide wall to the orbit, and is apparently fused with the upper surface of the palatine bone.



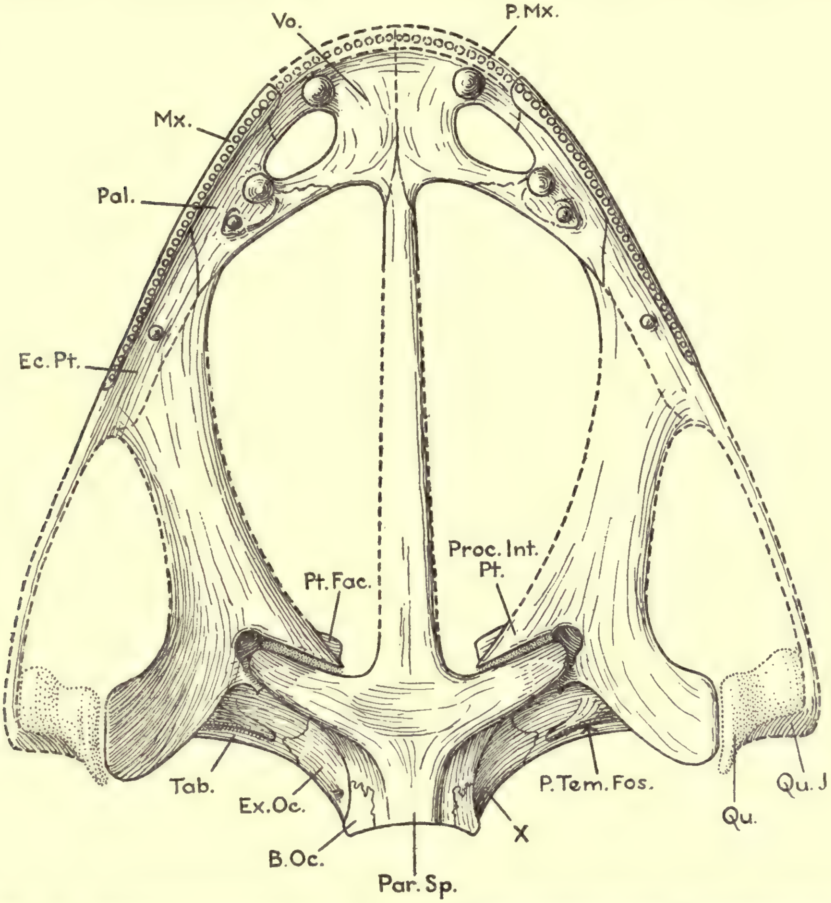
TEXT-FIG. 15.—*Eobrachyops townendae*. × 1⅓. Occipital aspect of skull viewed parallel to the dorsal surface. Reference letters as before with : *P.Tem.Fos.*, post-temporal fossa ; *Par.Ot.Pt.*, parotic flange of pterygoid ; *Par.Sp.*, parasphenoid ; *X*, foramen for the tenth cranial nerve.

The jugal forms the posterior and lower corner of the orbit, meeting the lachrymal in a suture which has been pulled apart so that the depressed surface, with an abrupt posterior ending which housed the hinder end of the lachrymal, is very clearly seen. Behind the orbit the jugal continues backward, between the postorbital and squamosal above, and the maxilla below, until it reaches the incompletely preserved quadratojugal.

The quadratojugal has a long exposure on the lateral surface of the skull, then turns in to continue downward the posterior surface of the squamosal.

## OCCIPUT

One of the more remarkable features of this skull is the amount by which the occiput extends behind the posterior border of the ornamented table. In consequence the occipital flanges of the dermosupraoccipitals are largely visible from above as a wide triangle with a truncated apex. These flanges are marked off by a transverse groove lying below and behind the rounded ridge, which is the hinder border of the table. Each flange is notched posteriorly by a groove which passes forward near the middle line below the skull roof. The lateral borders of the flanges stand out freely above the post-temporal fossae.



TEXT-FIG. 16.—*Eobrachyops townendae.* × 1⅓. The palate viewed at right angles to the parasphenoid. Reference letters as before with: *Ec.Pt.*, ectopterygoid; *Par.Sp.*, parasphenoid; *Proc.Int.Pt.*, processus internus of the pterygoid; *Pt.Fac.*, dorsally placed process of the pterygoid perhaps for the epipterygoid; *Vo.*, vomer.

The tabular has a very slender occipital flange, not visible from above, which stretches inward and downward behind the cartilaginous paroccipital.

In occipital view the basioccipital forms a large, concave condyle, the " articular " surface being spheroidal, though notched on its upper surface for the notochord. The lateral borders are rounded and thickened. The upper surface is largely covered by the lower ends of the exoccipitals, which send inward flanges (which probably did not meet) below the foramen magnum. The exoccipitals then rise as columns on each side of the foramen magnum, approaching one another until they are broken across and now show a damaged upper surface. Their apparent continuation over the summit of the foramen magnum is by a small bone (or bones) which is notched below, and extends down the sides of that opening so as to meet them with a continuous admesial surface, there being no trace of the step which in most Labyrinthodonts receives a cartilaginous supraoccipital. It is therefore likely that the bone in question is actually a supraoccipital. From its posterior surface each exoccipital extends forward and outward, surrounding the vagal foramen, and is perforated by two more ventrally placed small openings which (by comparison with *Capitosaurus*) may be for the XIIth cranial nerve. The rest of the bone clearly sheathed the posterior surface of the persistently cartilaginous paroccipital, whose position is fixed by that of the occipital flange of the tabular, which laterally sheathed its posterior face.

### PALATE

The parasphenoid is a remarkably large and elaborate bone. Its hinder margin reaches the rim of the single concave occipital condyle, and indeed appears to border the whole lower half of this structure, surrounding and hiding the basioccipital in ventral view. Laterally the parasphenoid ends in a suture with the exposed lateral surface of the basioccipital, but further forward this suture rises to cut the surface to which the ventral face of the exoccipital is attached. From this place the parasphenoid widens, its border passing outward and forward to help to form an immense basipterygoid process. In this region the bone is very shallowly concave mid-ventrally, but then rises a little so that the anterior face of the process becomes a deep and apparently vertical, transversely placed articular surface, which is applied to a corresponding facet on the pterygoid. Mesial of this articulation the border of the parasphenoid passes inward round the interpterygoid vacuity to extend anteriorly as the outer edge of a processus cultriformis. The bone is then concealed by matrix until what appears to be the ventral surface of its anterior end is exposed at the anterior end of the specimen. The parasphenoid behind the basipterygoid process has a nearly flat central region bounded on each side by a depressed area for attachment of recti capitis muscles over the lateral parts of the basioccipital.

The pterygoid bears a powerful " internal process " which passes inward from the meeting point of the palatal and quadrate rami. The straight borders of this process meet at a point directed mesially at the hindmost place on the border of the interpterygoid vacuity. This process is obliquely truncated by an apparently flat articular surface opposed to the corresponding face of the parasphenoid ; the two are separated in the specimen by a film of matrix about one millimetre thick. The front face of the articular process of the pterygoid is obviously continued outward and forward as the lateral margin of the interpterygoid vacuity. Lateral to and immediately behind the articular face the lower surface of the pterygoid is excavated by a smoothly rounded pit, which lies immediately lateral to the tip of the parasphenoid. The floor of this pit extends inward onto a thin shelf of bone separated, in the specimen, from the parasphenoid by about 2 mm. of matrix. It is in every way probable that this space was originally occupied by a cartilaginous basipterygoid process of the basisphenoid. Laterally the pterygoid turns down to form the border of the subtemporal fossa, and, with the much deeper surface of the quadrate ramus, makes a sheath to the temporal muscles, and bounds the characteristic U-shaped section of the palate.

Further back the short quadrate ramus of the pterygoid is abruptly produced downward as a deep flat sheet of bone with nearly parallel anterior and posterior edges. The posterior border, originally applied to a cartilaginous quadrate, lies along the hinder and inner border of the squamosal, but is throughout separated from it by a narrow space originally filled by the quadrate. Above the level of the inwardly directed shelf, which lies above the presumed cartilaginous basisphenoid, the parotic plate of the pterygoid rises vertically to, or very nearly to, the skull roof. The anterior end of this part of the ramus plunges into matrix.

The only other visible feature of the pterygoid is a small triangular shelf extending forward into the back of the interpterygoid vacuity from the anterior face of the articular process. This has a flat ventral surface, and lies high in the skull, presumably about at the level of the upper surface of the cartilaginous basisphenoid in its vicinity. It may have supported the foot of an epipterygoid.

No part of the palatal ramus of the pterygoid is exposed except for its anterior tip, seen through the orbit, which is grooved for attachment to the ectopterygoid and palatine. The ectopterygoid is only represented by a single large tusk, whose length is completely preserved.

The palatine bone is well shown. Its lateral border is throughout in contact with the inner surface of the maxilla, and its inner margin—forming part of the border of the interpterygoid vacuity—is completely visible. At its contact with the ectopterygoid the palatal exposure of the bone is extremely narrow. Anteriorly, at the level of the forward end of the vacuity, the bone bears two very large teeth; the anterior of these is a mature tooth of circular section, the tip being lost, the posterior was in process of growth, arising within a ring of bone standing out from the palatine. The crown of this tooth lies misplaced nearly horizontally and is sharp-pointed, of circular section, and longitudinally striated. Mesial of these teeth the bone extends inward, with a narrow exposure between the nostril and the vacuity, to reach and be overlapped by the vomer. Anteriorly to the teeth the palatine stretches forward internally to the maxilla until it meets the vomer, excluding the maxilla from the internal nostril.

The vomer is a large bone well shown on the right side of the specimen. Its contacts with the palatine have just been described; it forms part of the border of the interpterygoid vacuity, and has a process which extends backward along the lower surface of the parasphenoid. It bears one large tooth, of which only half the root is preserved.

The premaxillae have been broken away, but a small process of one of them, resting on the upper surface of the vomer, can be seen through the right external nostril.

The maxilla is a very shallow bone deepened anteriorly where it is attached to the septomaxilla. It ends anteriorly in an almost vertical suture with the premaxilla. Its lower border turns a little down posteriorly. It bears a series of small close-set teeth, apparently uniform and circular in section, sharp-pointed and unexpectedly high at the hinder end of the row.

## LATERAL LINE

Lateral line grooves are very poorly represented. There is a somewhat unusual groove which nearly surrounds the orbit. It begins about at the suture between the prefrontal and lachrymal, and passes over the pre- and postfrontals and the postorbital on to the jugal, along which it passes—apparently just touching the lachrymal and then descending on to the maxilla. There is a possible short branch crossing the postorbital towards the intertemporal. The rest of the skull and the lower jaw seem to lack any trace of these structures.

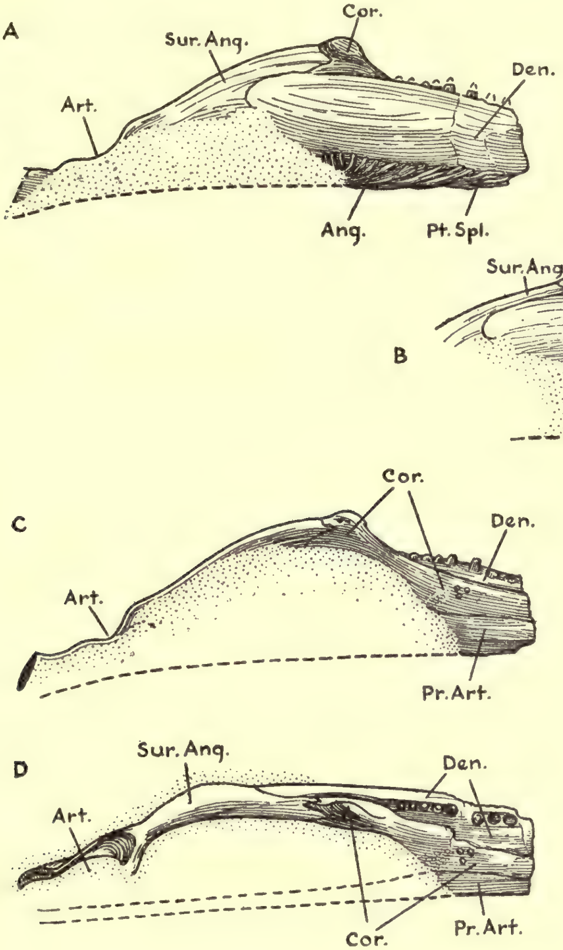
## LOWER JAW

The hinder part of the left lower jaw is preserved, but is largely concealed by irremovable matrix. It is of normal Labyrinthodont structure, but possesses some unusual features. There is every reason to believe that its lower border was straight ; there is a relatively long retroarticular process, a marked coronoid process, and a lightly ossified articular. The angular is the usual boat-shaped bone with a radiating ornament of ridges, and the hinder end of what is presumably the postsplenial is similarly ridged. Little but the upper border of the surangular is exposed. This bone extends back along the outer surface of the retroarticular process, in front of which its upper edge bears a rounded notch marking the position of the articular surface. From the anterior end of this notch a process passes inward, which laterally carries a small part of the articulation for the quadrate, whilst mesially it seems to have sheathed the front of the partly cartilaginous articular. The upper border of the bone outside the supra-meckelian fossa is thick and rounded, ending at a clearly marked suture with that hinder end of the coronoid which forms a definite process with a narrow but rounded summit. The outer surface of the surangular has no ornament so far as can be seen, and the dentary overlaps it.

The dentary reaches the ornamented surface of the angular and the postsplenial. Its outer surface is rounded from dorsal to ventral edges, and is perfectly smooth. The narrow dentigerous border supports a single row of small, close-set teeth of circular section. Anteriorly a smooth surface of the dentary lies above the coronoid on the inner surface.

The coronoid is applied to the inner surface of the dentary, rising to its process, where it is wedged into the surangular. It surrounds the anterior end of the supra-meckelian fossa and stretches forward on the inner surface of the jaw as far as the specimen extends. This surface bears a patch of three small hemispherical denticles, but is otherwise smooth. Its lower border rests on the prearticular.

The prearticular is represented by a section of its hinder end separated by a space (which represents the cartilaginous articular) from the retroarticular part of the surangular. Anteriorly its lower margin is overlapped by the postsplenial.



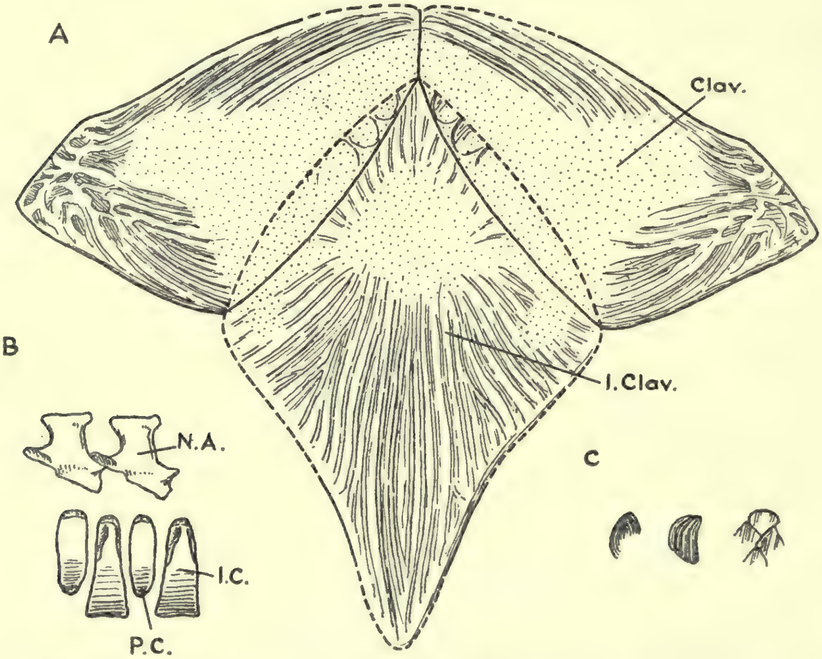
TEXT-FIG. 17.—*Eobrachyops townendae.* × 1⅓. The hinder part of the lower jaw. A, Right side, external aspect; B, right side viewed somewhat from below; C, left side, from within; D, left side from above. *Ang.*, angular; *Art.*, articular; *Cor.*, coronoid; *Den.*, dentary; *Pr.Art.*, prearticular; *Pt.Spl.*, post splenial; *Sur.Ang.*, surangular..

The very much bowed upper edge of the lower jaw makes it difficult to determine its relation to the skull. It seems, however, clear that the jaw was so placed that the lower border was turned in, the flat inner surface facing partly upward. Such a position brings the upper part of the outer surface of the dentary (below its tooth bearing edge) vertical, as it should be, and places the little of the articular cavity that can be seen in a reasonable position.

### VERTEBRAL COLUMN

The vertebral column is represented by a single neural arch and a number of "central" bones. All these are fractured and incomplete, but, so far as they go, are well preserved.

The neural arch seems not to have been co-ossified with its fellow of the other side; it has a considerable neural spine expanded fore and aft at its summit. This spine arises from an elongated body, along the side of the neural canal, bearing narrow pre- and postzygapophyses which have no special character. The lower border of the bone is broken and does not show the way in which it articulated with the central elements. There is, however, a short, anteriorly placed transverse process.



TEXT-FIG. 18.—*Eobrachyops townendae.* × 1⅓. A, Reconstruction of the dermal shoulder girdle from below. Areas in which the ornament is represented are seen on one side or the other, borders in broken line restored, dotted area has not been seen on either side, being hidden by matrix or other bones (its shape has no significance). B, Reconstruction of two vertebrae from the right side; C, various scales. *I.C.*, intercentrum; *N.A.*, neural arch; *P.C.*, pleurocentrum; *Clav.*, clavicle; *I. Clav.*, interclavicle.

There are about a dozen incomplete circum-notochordal bones, all so much alike that I have been unable to distinguish intercentra from pleurocentra with certainty. They clearly surrounded a large notochord of the order of 8 mm. in diameter, their outer surface being composed of dense bone with a good surface which tends to be turned a little outward anteriorly and posteriorly. The bone is thin, about 1 mm.

thick, and the inner surface is slightly roughened and not covered with dense periosteal bone. All the fragments which show a natural termination end in a rounded point extending beyond the periosteal outer surface. Those bones which I regard as intercentra narrow dorsally from a maximum of 4·5 mm. to some 2 mm. in a height of 8·0 mm. In all cases the wide ventral end is a fracture, and it seems probable that the bones were really large segments of a cylinder and were not paired. These bones show a narrow but rather deep flattening on the posterior part of the upper end of their outer surface, which is presumably a rib-facet.

One bone, which seems to be complete, is 8 mm. high and has a maximum width of 2·5 mm. It is seen from its inner surface and is presumably a pleurocentrum. In Text-fig. 18 I have made a restoration of two vertebrae on the basis of the remains described above, and it may be mentioned as a point in its favour that it fits the occipital condyle.

## SHOULDER GIRDLE

The interclavicle and right clavicle are nearly complete, but are in part hidden by matrix. The area of the ventral surface of the interclavicle on which ornament is shown in Text-fig. 18 is exhibited on one or other side of the specimen, and its middle line is fixed by a marked median ridge on the visceral surface of its anterior end. Occasional short lengths of genuine margin, or of the overlap surface for the clavicle, fix its shape within narrow limits. The right clavicle, seen from its ventral surface, is very nearly complete, but much of it is covered by matrix and other bones.

Thus the restoration rests on adequate evidence, and it seems to be certain that the clavicles must have met for a considerable distance in front of the interclavicle. It will be noted that the total width fits neatly that of the skull. The height and direction, though not the structure of the dorsal process of the clavicle, is known; it stands up at right angles to the ventral surface of the bone and is 22 mm. high, leaving room in the body for a cleithrum of normal proportions.

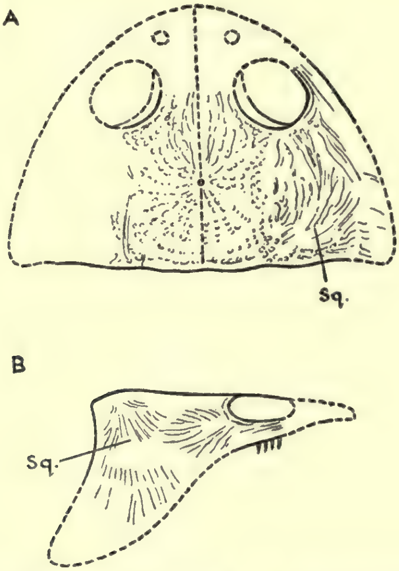
## SCALES

In a number of places groups of small, oval, ? bony scales may be seen (Text-fig. 18). Each has an ornament of low concentric ridges. They appear to have overlapped extensively, and are about 3 mm. across, but very thin.

## POSSIBLE RELATIONSHIP TO ACHELOMA CASEI AND TRIMERORHACHIS

The only animal to which the Labyrinthodont described above has any similarity is that described by Broili in 1913 as "*Acheloma*" *casei*. The two specimens agree in that they have a truncated posterior border to the dermal skull, with no trace of an otic notch. In both the orbits lie far forward, with a well marked smooth border surrounding each, and are not exceptionally close together. Broili's lateral view seems to show a tooth-bearing fragment of maxilla not far below the orbit, and shows that the cheek was deep. Indeed the two skulls not only resemble one another in general shape, but in the character of their ornament and the general direction of the ridges on the cheek bones which form it. They may well belong to the same genus.

But they are specifically different. The new skull has a large, transversely widened pineal foramen, "*Acheloma*" *casei* a very small one. The table of the new skull is broader than it is in Broili's specimen, and so is the interorbital space, whilst the orbit of "*Acheloma*" *casei* is wider than that of the new form. The squamosal in "*Acheloma*" *casei* appears to be deeper than that of my animal, and the new skull being only some twenty-five per cent larger than the old, it is impossible to explain the visible differences in proportion as due to growth. I propose to call the new specimen *Eobrachyops townendae* gen. et sp. nov. *Eobrachyops* expresses my opinion of its systematic position, *townendae* is in honour of Miss Joyce Townend, who made the drawings which illustrate this and all my other recent work. "*Acheloma*" *casei* Broili becomes *Eobrachyops casei*.



TEXT-FIG. 19.—*Eobrachyops casei* (Broili). × ⅔. Reconstruction of the skull drawn from Broili's figures, left side copied from right. The outline of the cheek in B, hypothetical, is based on a comparison of the ornament shown on it with that of *E. townendae*. A, Dorsal surface ; B, right lateral surface. *Sq.*, squamosal.

*Eobrachyops* comes from an unknown locality and horizon but belongs to the Cope collection, much of which came from the Wichita formation, though some is Clear Fork. Professor A. S. Romer has examined the specimen of *E. townendae* and tells me that the matrix is certainly Clear Fork, as is *E. casei* It now bears the number Amer. Mus. 2455.

The only contemporary form which resembles it at all is *Trimerorhachis*.

*Trimerorhachis* has been described by Cope, Broili, Case, Broom and Williston, but still needs much further description. I therefore give a further account of the basicranial and otic regions.

The two genera have in common: a skull which is depressed, at any rate anteriorly, anteriorly placed orbits, an intertemporal bone in the table, a shallow (or absent) otic notch, an occipital condyle, the greater part of which is made by the basioccipital —so that it is deep and has a concave articular face—and a " movable " articulation between the basipterygoid process of the parasphenoid and the pterygoid.

## TRIMERORHACHIS

### Variation of Specimens

The following account is founded on four specimens which Professor Romer was good enough to send me (M.C.Z. 1169, 1975 A, B & C); and on B.M.N.H., R.576, which reached the Museum in 1885, from the collection of Waldemar Kowalevski, to whom it had been given by E. D. Cope before 1883 (as is recorded in a letter dated 30.vii.1885 from Cope to Henry Woodward in the archives of the Geology Department of the British Museum).

The skull of *Trimerorhachis* is generally believed to have been very much flattened, as much so perhaps as in a late Triassic Stereospondyl. But it seems certain that this flattening, in some cases at any rate, did not extend to the occiput, although it did to the quadrate regions of the skull.

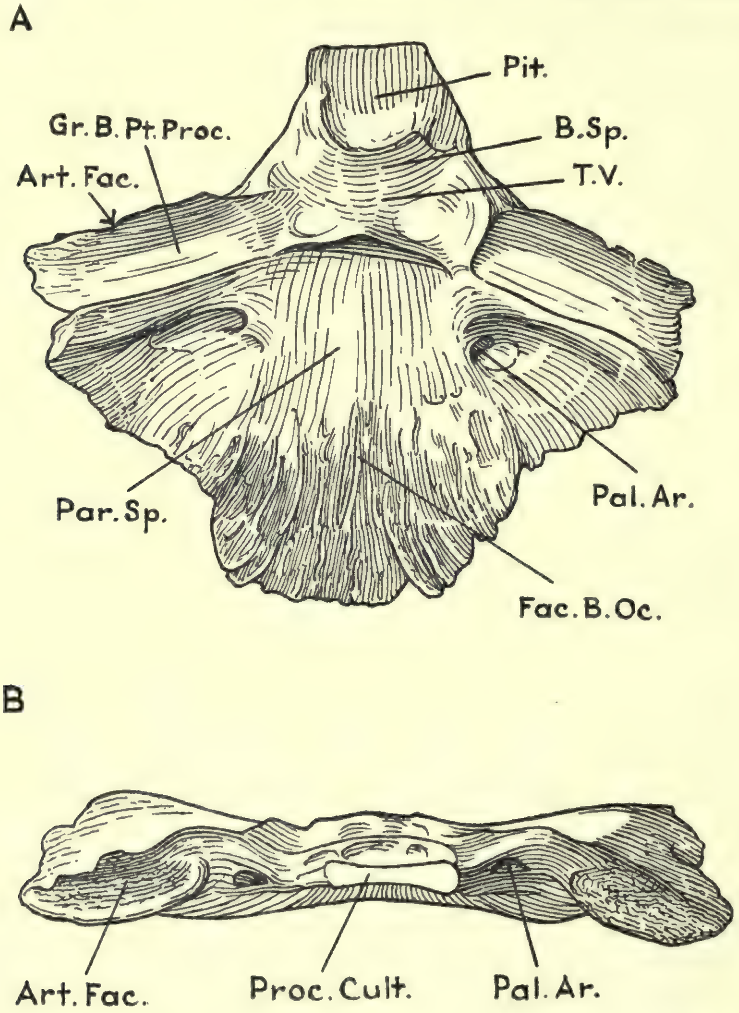
The occipital condyle is always single, and concave, but it varies a good deal in shape in different specimens—perhaps from different horizons. In one specimen before me it measures 2·3 cm. transversely, and is 1·75 cm. high. Another is 2·25 by 1·5 cm., the outline being convex throughout. Another is 2·1 by 1·6 cm. and has concave lateral borders below the middle of its height, whilst R.576 is 2·1 cm. wide and only 1·2 cm. high, the basioccipital part of the structure being greatly reduced. These variations are obviously related to the general flattening which takes place with time in Labyrinthodonts. Associated with them is a change in the height of the exoccipital above its condylar portion. In the second of the above specimens the height is 1·3 cm., in the third 1·2 cm., and in the fourth only 0·75 cm., in other words the flattening is general.

One of the specimens mentioned above (M.C.Z. 1169) has the table of the skull well preserved and visible from both upper and lower surfaces and from the back. The dermosupraoccipital bears a very obvious occipital flange 1·05 cm. deep, and this " flange " is merely the occipital exposure of a thick mass of bone whose lower surface, which lies nearly horizontally, extends forward for nearly a centimetre and obviously rested directly on the upper end of cartilaginous continuations of the exoccipital, and the paroccipital. There is no evidence of any overlap of the dermosupraoccipital on the occipital surface of the exoccipital. Thus the minimum height of the occiput is 1·6 (condyle) + 1·2 (exoccipital) + 1·05 (postparietal flange) = 3·85 cm. (assuming—as we justifiably may—that it was vertical) and the width of the table between the otic notches directly measured is 6·3 cm., i.e. as 1 : 1·64.

*Eryops* in Sawin's figure is 1 : 2·43. In fact the occiput of *Trimerorhachis* is deeper and narrower than that of *Eryops* and even of *Edops*.

## BRAIN-CASE

The basioccipital is a wedge-shaped bone forming the lower part of the single occipital condyle. It has a short, free ventral surface posteriorly which extends



TEXT-FIG. 20.—*Trimerorhachis* sp. (M.C.Z., 1975). × 2. Posterior part of the parasphenoid, with co-ossified basisphenoid. A, From above ; B, from in front. *Art.Fac.*, articular face on the parasphenoid for the processus internus of the pterygoid ; *B.Sp.*, basisphenoid ; *Fac.B.Oc.*, ridged face for attachment of the basioccipital ; *Gr.B.Pt.Proc.*, groove for the cartilaginous basipterygoid process ; *Pal.Ar.*, foramen for the palatine artery ; *Par.Sp.*, parasphenoid ; *Pit.*, depression for the pituitary body ; *Proc.Cult.*, processus cultriformis of the parasphenoid cut across ; *T.V.*, transverse vein.

outward to smooth lateral surfaces, usually concave, which terminate dorsally at the attachment of the exoccipital. The greater part of the ventral surface is ridged for the overlap of the hinder part of the parasphenoid, which turns upward round the bone to continue its concave lateral faces forward over a suture, so forming a deep pocket, presumably for the attachment of a recti capitis muscle. The dorsal surface of the basioccipital has a median groove for the notochord, lateral to which lie the facets for the exoccipitals, whilst anteriorly the bone thins until it gradually fades away into the upper surface of the parasphenoid.

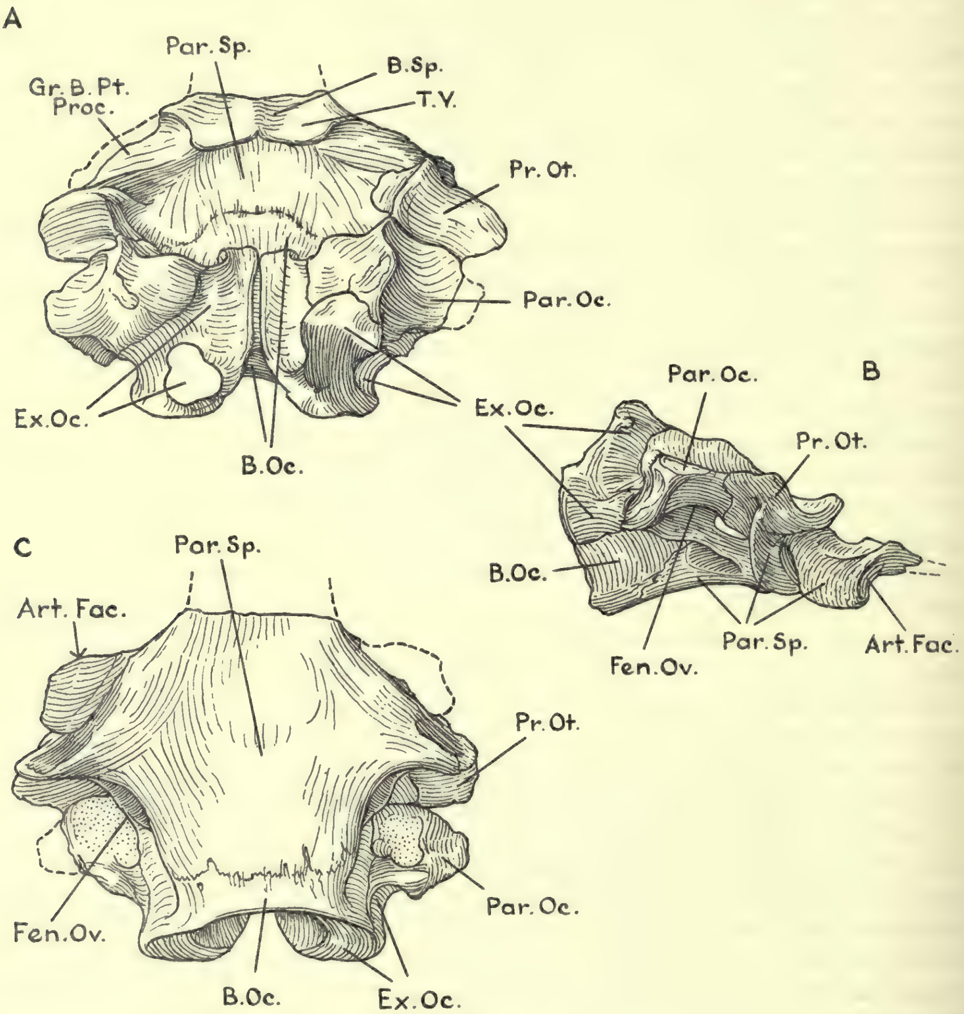
The parasphenoid is directly comparable with that of *Eryops* or—perhaps more easily—a primitive Neorhachitome. It varies a good deal in shape in different individuals, but these changes merely overlie a fundamental uniformity. On its upper surface the parasphenoid at the root of the processus cultriformis is co-ossified with an extremely thin basisphenoid. No dividing line between the two bones can be seen in section, but that the basisphenoid does indeed exist is shown by surfaces belonging to it not covered by perichondral bone, but formerly continued by cartilage. These exist posteriorly toward the basioccipital, and laterally at the base of the grooves, lying on the upper surface of the articular process, and bounded behind by the lateral ridge, which show the position of cartilaginous basipterygoid processes. Consideration of the facet on the pterygoid for these processes suggests that the cartilage was shallow, the functional articulation being between the parasphenoid and the pterygoid.

The dorsal surface of the body of the basisphenoid has a shallow concavity bounded by a transverse ridge behind, which agrees with a similar structure in *Eryops*, on whose floor Sawin held that the recti muscles had their origin. Further forward on the upper surface, at the root of the processus cultriformis, lies a depression for the pituitary, as in *Eryops*. Behind the lateral ridge on the upper surface of the parasphenoid is a smooth depression, passing out laterally, which no doubt sheathed the lower part of the proötic. In one specimen (but not in R.576) a small foramen enters the bone from the admesial end of this hollow.

The exoccipital has a base which is closely attached to, and ultimately fuses with, the upper surface of the basioccipital. This base is moulded on the upper surface of the notochord, its posterior surface forming part of the great concave " condyle ". It expands inward to floor the brain cavity and nearly (or quite) meets its fellow in the middle line. The base extends forward and a little outward until it ends abruptly at a face presumably lying in contact with the lower cartilaginous portion of the paroccipital. Anteriorly the upper surface of the base forms the floor of the vagal foramen, whose posterior wall is the massive ascending part of the exoccipital which bounds the foramen magnum. It is important to note the complete absence in *Trimerorhachis* of that perichondral extension of the exoccipital, which in *Eryops* and all its successors overlaps the paroccipital to an ever-increasing extent. The hinder surface of the exoccipital which rises to the dermosupraoccipital is essentially flat, but it bears a small protuberence a little above the level of the floor of the foramen magnum. This recalls the facet for attachment of a proatlas in many reptiles and may have had this function, for processes for the attachment of such a bone exist on the anterior faces of the atlantal neural arches (Cope & Matthew, 1915, pl. 8, fig. 1b).

The upper end of the exoccipital is abruptly truncated and no doubt continued by cartilage.

The paroccipital is well shown in three of my specimens. It is a large bone with the posterior surface covered by a smooth perichondral layer. The admesial part of its posterior surface forms a stout pillar, ending below in a rounded and laterally


A
Par. Sp.
Gr. B. Pt. Proc.
B.Sp.
T.V.
Pr. Ot.
Par. Oc.
Ex.Oc.
Ex.Oc.
B.Oc.
B
Par. Oc.
Ex.Oc.
Pr. Ot.
B.Oc.
Fen.Ov.
Par. Sp.
Art. Fac.
C
Par. Sp.
Art. Fac.
Pr. Ot.
Fen.Ov.
Par. Oc.
B.Oc.
Ex.Oc.

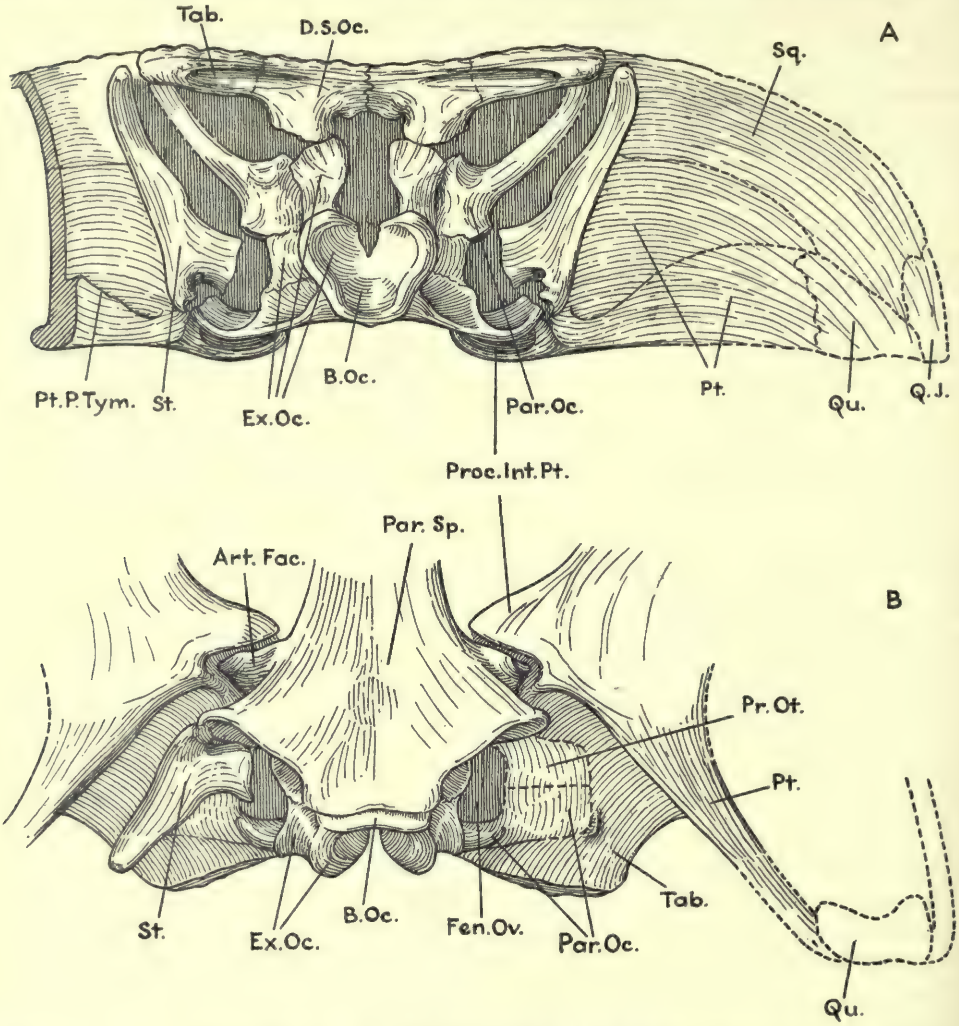
Text-fig. 21.—*Trimerorhachis* sp. (B.M.N.H., R.576). × 1½. Posterior part of the parasphenoid with hinder part of the brain-case articulated with it (compare with Text-fig. 20). A, From above; B, from the right side; C, from below. Reference letters as before with: *B.Oc.*, basioccipital; *Ex.Oc.*, exoccipital; *Fen.Ov.*, fenestra ovalis; *Par.Oc.*, paroccipital; *Pr.Ot.*, proötic.

widened mass clearly originally continued by cartilage, which is applied to—but extends laterally of—the front end of the base of the exoccipital. A groove on its hinder surface passing forward and inward completes the vagal foramen, and the upper end of the bone must touch the exoccipital and nearly reaches the skull roof. The bone is continued laterally by a massive paroccipital process, which is thin dorso-ventrally but wide from back to front. The outer end of this process is unossified, but clearly extended laterally as cartilage to be received in a depression on the lower surface of the tabular bounded laterally and posteriorly by an upstanding ridge. This depression lies far in front of the corner of the tabular at the inner side of the otic notch. Throughout the paroccipital is widely separated from the skull roof by a large post-temporal fossa. The lower surface of the paroccipital process is only shown in R.576, where it extends forward to meet the corresponding surface of the proötic, and admesially ends abruptly in a border lying parallel with the middle line, which is the upper margin of the bony fenestra ovalis.

The proötic is ossified in R.576. It is a bone much resembling the paroccipital, to which it is closely applied, the two together forming a wide but shallow process, with a wide groove running antero-posteriorly above it, which flares out on to the shallow anterior face of the proötic. Ventrally the proötic has a base descending into a mass of cartilage resting on the parasphenoid, and it forms the anterior part of the fenestra ovalis.

The stapes lies nearly in position on each side of one specimen (M.C.Z. 1169), from which Text-fig. 22 is drawn. In it the stapes is placed in position and is necessarily foreshortened. The bone has an almost straight outer border, which turns in at its lower end to the accessory process. The shaft of the bone is gently concave across its lower (posterior) surface, rounding over on the outer side, the inner forming a distinct edge. The inner border bows out from the bone a little in the middle of its length, but cannot have come into contact with the otic capsule. Distally the bone ends in a small rounded surface, whilst proximally the powerful accessory process turns a little inward and ends in a surface, at about 45 degrees to the length of the bone, which is itself thrown out into minor processes for an attaching ligament. This process is separated by a groove, into which opens the foramen for the stapedial artery, and a notch from the more powerful process which carries the footplate. This process passes inward at an angle of about 130 degrees to the shaft, is massive, and truncated by a slightly concave surface for attachment to the membrane closing the fenestra. It seems evident that this ancillary process was connected to the outer end of the lateral ridge of the parasphenoid, and that the distal end of the bone lay in the tympanic membrane, the footplate being thus brought squarely into the obvious position of the fenestra ovalis.

The pterygoid has a remarkable mode of articulation with the basis cranii. It is evident that the important attachment was between a face directed backward, and placed vertically on the posterior surface of a special inwardly directed process of the pterygoid, and the front face of the parasphenoidal process. Each of these two opposed facets is concave, so that it is evident that the joint—though firmly fixed—was flexible owing to the presence of a ligamentous pad between the two bones. The outer end of the posterior border of the articular process of the pterygoid swings round so as to limit a pit whose hinder wall is the beginning of an ascending rounded ridge passing upward and backward at the root of the quadrate ramus. Little space is left for a contact between the cartilaginous basipterygoid process and the pterygoid. Apart from the special articular process (not otherwise known in described Texas Labyrinthodonts) the pterygoid generally resembles that of *Eryops*, though it possesses the groove bounded by a ridge on the posterior surface of the


Tab.
D.S.Oc.
A
Sq.
Pt.P.Tym.
St.
Ex.Oc.
B.Oc.
Par.Oc.
Pt.
Qu.
Q.J.
Proc.Int.Pt.
Par. Sp.
Art. Fac.
B
Pr.Ot.
Pt.
Tab.
St.
Ex.Oc.
B.Oc.
Fen.Ov.
Par.Oc.
Qu.

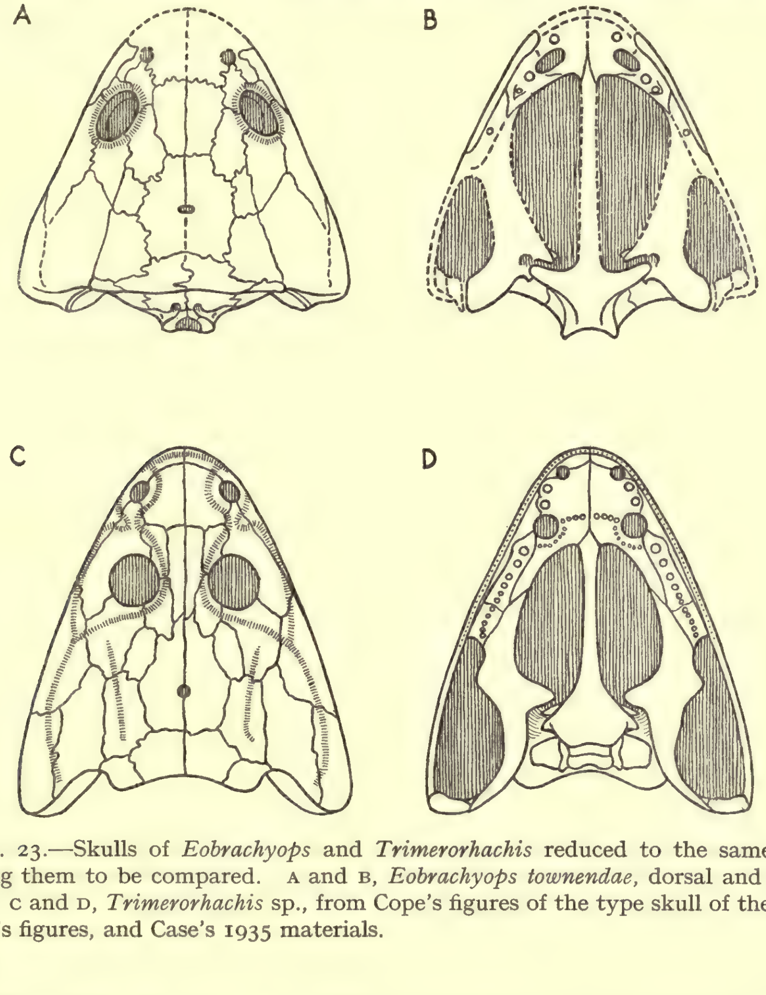
TEXT-FIG. 22.—*Trimerorhachis* sp. Reconstruction of the posterior part of a skull made from specimen M.C.Z. 1169. About natural size. A, From behind; B, from below (to be compared with Text-figs. 20 and 21). Reference letters as before with: *D.S.Oc.*, dermosupraoccipital; *Proc.Int.Pt.*, processus internus of pterygoid; *Pt.*, pterygoid; *Pt.P.Tym.*, post-tympanic ridge of the pterygoid; *Qu.*, quadrate; *Q.J.*, quadratojugal; *Sq.*, squamosal; *St.*, stapes; *Tab.*, tabular.

quadrate ramus, originally recognized by Sushkin as the floor of the tympanic cavity in *Capitosaurus*. The remainder of the structure of *Trimerorhachis* is well described by Cope, Broom, Williston and Case.

## COMPARISON OF EOBRACHYOPS WITH TRIMERORHACHIS

### Resemblances

*Eobrachyops* and *Trimerorhachis* are not very different in size; the type skull of *T. conangulus* Cope is about two-thirds as long as *E. townendae*, whilst most specimens of *T. insignis* are twice the size. The two animals resemble one another in the general outline of the skull, in the forward position of the orbits, and in their flat dorsal surfaces. The otic notches are small in *Trimerorhachis*, and absent in *Eobrachyops*. An intertemporal bone is present in each. The occipital condyle of each is a nearly circular concave face, largely made by the basioccipital. In each the pterygoid



Text-fig. 23.—Skulls of *Eobrachyops* and *Trimerorhachis* reduced to the same width enabling them to be compared. A and B, *Eobrachyops townendae*, dorsal and palatal views; C and D, *Trimerorhachis* sp., from Cope's figures of the type skull of the genus, Broom's figures, and Case's 1935 materials.

articulates "movably" with the parasphenoid by transverse faces. In each a pocket—apparently for the insertion of the recti capitis muscle—lies on the lateral surface of the parasphenoid not very far behind the articulation with the pterygoid. In each form the mandible is remarkable at this period in possessing a well-developed retroarticular process.

The vertebral columns are similar in the lack of fusion of the two halves of the neural arches in the anterior region, in the delicacy of the circum-notochordal elements, and in the large size of the notochordal sheath. The dermal shoulder girdles are similar in the presence of rhomboidal interclavicles, and in the wide expansion of the ventral parts of the clavicles, a condition otherwise unknown in the Texan Permian Labyrinthodonts—except in *Archeria* (= "*Cricotus*"). The two forms possess identical bony? scales. There is therefore a number of real resemblances between the two forms, and a further analysis is necessary.

## DIFFERENCES

The resemblance in general skull outline is purely superficial. The small otic notch of *Trimerorhachis* housed a tympanic membrane in which the stapes ended, *Eobrachyops* must have entirely lacked such a structure, no doubt a secondary condition associated with some change in the mechanism of hearing.

In *Eobrachyops* the quadrate lies far forward on the level of the occipital condyle, in *Trimerorhachis* it is relatively far back, at least in some specimens. In *Eobrachyops* the quadrate articulation is carried down by the deep cheek and lies far below the floor of the basioccipital, whilst in *Trimerorhachis* the quadrate condyle seems to be on the same level as the bottom of the occipital condyle.

In *Eobrachyops* the orbits are widely separate from one another and extend so far laterally that the depth of the jugal and maxilla below them is extremely small. In *Trimerorhachis* conditions are quite different, the face below the orbit being very deep. In the detail of pattern of dermal bones in the circumorbital region the two animals differ very greatly. In *Trimerorhachis* the lachrymal is a huge bone, extending from the nostril backward below the orbit to meet not only the jugal, but the postorbital. In *Eobrachyops* it forms scarcely more than one half of the outer border of the orbit, and does not reach the nostril.

Thus the occurrence of an intertemporal in each form is merely the retention of a primitive character, and there is no reason to suppose that the few resemblances between the skull roofs have any phylogenetic significance ; they have been derived, no doubt, from a common ancestral pattern by entirely different courses of change.

The basicranial and otic regions differ in the larger contribution which the exoccipitals make to the condyle in *Trimerorhachis*, and in the fact that in that animal there is no extension of the exoccipital over the paroccipital, whilst in *Eobrachyops* there is to such an extent that the vagal foramen lies entirely in the exoccipital. In *Eobrachyops* the paroccipital remains entirely cartilaginous, in *Trimerorhachis* it is well ossified.

In *Trimerorhachis* there is a special process from the parasphenoid which bears the articular face for the pterygoid, but in *Eobrachyops* this face is carried directly on the front of the great lateral wing of the parasphenoid.

The palate of *Eobrachyops* has larger interpterygoid vacuities than that of *Trimerorhachis*, as shown by the fact that the pterygoid does not meet the vomer. The two differ in the details of the dentition, and *Eobrachyops* is unique in that the vomer and palatine meet laterally to the internal nostril.

The lower jaw of *Eobrachyops* differs markedly from that of *Trimerorhachis* in its straight ventral border. The circumchordal elements of the vertebral column of *Eobrachyops* differ from those of *Trimerorhachis* in the much more parallel sides of the intercentra, which do not possess the typical rhachitomous wedge-shaped form of the latter genus. In the shoulder girdle the clavicles meet in front of the interclavicle in *Eobrachyops*, and not in *Trimerorhachis*.

## Two Striking Common Features

Thus it appears that the two genera are not very closely related : their resemblances are dependent on the retention of primitive qualities and a somewhat similar skull shape. However, the special process of the pterygoid which articulates with the parasphenoid is common to both, and is a very unusual feature ; and the retention of a deep basioccipital as the greater part of the nearly circular condyle, whilst the basisphenoid is so greatly dorso-ventrally depressed that the movable attachment of the pterygoid to the basis cranii is essentially by means of a special facet of the parasphenoid, is a remarkable point of resemblance between the two genera, as it seems to be found in few other animals.

## Characteristics of Eobrachyops are the Special Qualities of Brachyopids

The most striking special characteristics of *Eobrachyops* are (*a*) that the occipital condyle lies considerably behind the posterior margin of the skull roof ; (*b*) that the border of the pterygoid at the subtemporal fossa is suddenly carried upward so that the palate in this region is a broad ∩-shaped arch ; (*c*) that the quadrate condyle lies far below the ventral surface of the parasphenoid ; (*d*) that a distinct space, formerly occupied by a cartilaginous ridge on the posterior surface of the quadrate, separates the hinder border of the pterygoid from those of the squamosal and quadratojugal ; (*e*) that the outer surface of the squamosal and quadratojugal passes round on to the posterior face of the quadrate and there forms a laterally concave, nearly vertical surface.

These five characters are essentially those which I listed in 1919 (pp. 47–48) as special qualities of the Brachyopidae. Their occurrence in *Eobrachyops* and in no other Labyrinthodont except the Brachyopids and *Dvinosaurus* seems to me strong evidence for believing that *Eobrachyops* was the " prototype " of this group, in the sense that it was a Lower Permian representative rather than literally ancestral to any one of the later members.

## CONCLUSION ON RELATIONSHIP OF EOBRACHYOPS TO TRIMERORHACHIS AND BRACHYOPIDS

It is evident that *Eobrachyops* more greatly resembles *Dvinosaurus* and the Brachyopids than does *Trimerorhachis*. The latter lacks any sign of the deepened cheek which exists in all Brachyopids, and to a less extent in *Dvinosaurus*. It has often a considerable production of the quadrate condyle behind the occipital condyle, in contrast to the condition in Brachyopids. In *Trimerorhachis* the occiput is invisible from above (or nearly so) in contrast to the sloping occiput and very posteriorly placed condyles of Brachyopids, *Dvinosaurus* and *Eobrachyops*. In *Trimerorhachis* the pterygoid at the inner border of the subtemporal fossa is bowed inward mesially to the inner surface of the jaw, and is not at all produced downward. In *Dvinosaurus* this border is . . . " strongly inclined ventralwards by its end correspondingly to the general vaulting of the palatal surface " (Sushkin, 1936 : 56), but it does leave a small part of the subtemporal fossa visible within the lower jaw. The pterygoid of the Brachyopids differs from that of *Trimerorhachis* in ways which carry the differences shown by *Dvinosaurus* to their logical conclusion, but *Eobrachyops* has the Brachyopid condition in an extreme form.

In *Trimerorhachis* there is a functional otic notch, and a stapes of normal Labyrinthodont type ending in it. In *Dvinosaurus* and *Batrachosuchus* the stapes is greatly deepened distally, its end being tied down by ligament to that posterior surface of the ridge of the quadrate which separates the occipital part of the squamosal from the pterygoid. It is indeed not easy to imagine intermediate stages between the two conditions, whilst the resemblance between the stapes of *Dvinosaurus* and that of *Batrachosuchus* is obvious (cf. Sushkin, 1936 : 59).

In *Trimerorhachis* the lachrymal is immensely enlarged and separates the orbit widely from the maxillary border, in *Dvinosaurus* (Bystrow, 1938) it is less extensive and the space between the orbit and the maxillary border smaller. In Brachyopids it is still further reduced.

The comparison can be extended to many other features with the same conclusion : that *Trimerorhachis* may well have some real relation to *Eobrachyops*, but that the latter in all ways makes a better ancestor for *Dvinosaurus* and the Brachyopids.

## EOBRACHYOPS COMPARED WITH PELION

Sushkin, when he recognized the remarkable processus internus of the pterygoid of *Dvinosaurus* and showed its resemblance to that of *Trimerorhachis*, could only add as a parallel *Archegosaurus* as I figured it (1919, fig. 2). But it also occurs in the Coal Measure *Saurerpeton* and *Erpetosaurus* described by Romer (1930, 1947) and Steen (1931). I therefore examined Steen's materials of these animals in the British Museum. Dr. Steen had prepared them by removing the surviving remnants of bone by hydrochloric acid, thus getting exquisitely perfect impressions from which she could make squeezes in plasticene or dental wax only. But, as Mr. Donald Baird of Harvard showed me, it is possible to make casts from such moulds with rubber latex loaded with an opaque powder. Casts so made are incomparably better than any at Dr. Steen's disposal, and enable me to add some details to her perfectly accurate accounts of these animals.

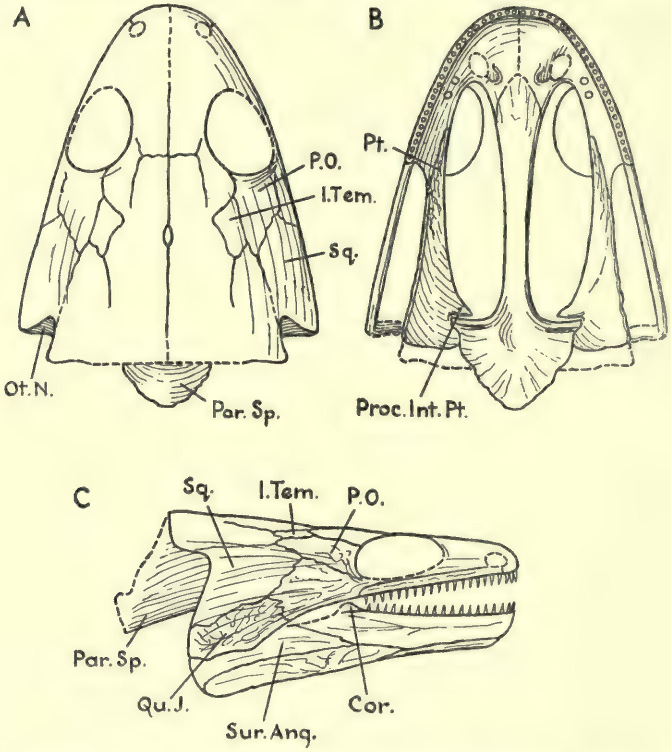
## IDENTIFICATION OF PELION LYELLI

Specimen B.M.N.H., R.2674, was described as *Pelion lyelli*, though Dr. Steen (1931: 874) notes that it differs materially from Romer's description of two skulls referred to that species in 1930. In 1947 Romer (without resolving the differences which Steen mentions) refers the three specimens in question to Moodie's genus *Saurerpeton*, founded on one of the specimens. *Pelion lyelli* has as type a partial skeleton so covered by a film of matrix that no real knowledge of its skull structure can be gained.

To *Pelion* Romer (1947) now refers a skull (described by Moodie as *Erpetosaurus tabulatus*) for which he founded a genus *Branchiosauravus* in 1930. Romer (1930, fig. 7) draws (but leaves unshaded) a bone projecting behind the table. This bone in Moodie's photograph (1916, pl. 25, 2) seems to lie below the skull roof and to have a pair, less evident, but a good match. It is possible that these are the remains of an occiput, stretching backward behind the occipital border of the table as that structure must have done in Steen's *Pelion*. Thus it is probable that the two animals belong to the same species, Moodie's being older than Steen's, as it is half as large again.

## RE-EXAMINATION OF PELION

Steen's specimen of *Pelion lyelli* may be described from the cast as follows. The skull lies on its dorsal surface, both lower jaws being in position, articulated with the quadrate condyles. On the spectator's right (animal's left) side the cheek is completely flattened out into the plane of the table, the lower jaw is seen—dorso-ventrally compressed—directly from below, but with the border of the pterygoid at the sub-temporal fossa squeezed down into contact with its inner surface. This crushing has disarticulated the pterygoid from the basis cranii, which, although crushed down on to the skull roof, is still nearly symmetrically placed with respect to the eyes. The right lower jaw is in articulation with the quadrate, but has become detached at the symphysis and straightened, by pressure, lies so as to show the whole of its outer surface. Its lower border has squeezed and broken the lower part of the pterygoid where it forms the border of the sub-temporal fossa. The right maxilla, jugal and quadratojugal lie in nearly natural articulation with each other and with the quadrate and lower jaw, and are inturned so that their outer surface is shown. Steen, in her accurate drawing (text-fig. 15), shows the large parasphenoid with a rather definitely marked short blunt-ended basipterygoid process. The new cast shows that this structure has its anterior edge drawn downward, so that there is a large somewhat concave face directed forward to which a corresponding facet of the pterygoid was attached. On the spectator's left the corresponding process is shown with a special " processus internus " of the pterygoid in articulation with its flat front face. On the spectator's right Steen's fig. 15 shows quite accurately a strange hook-shaped mesial edge to the pterygoid, which in her restoration she attached to the outer end of the parasphenoid process, but in the same figure she shows with a dotted line a break in the inner border of the palatal process of the pterygoid. It is evident from the new cast that this is the real processus internus, with a flat surface directed backward for articulation with the anterior deepened face of the parasphenoid, the whole agreeing exactly with the structure seen on the animal's right. The pterygoid extends outward from this articulation as a relatively enormous sheet of bone somewhat cracked and crumpled but evidently continuous to a border, which is pressed against the inner surface of the lower jaw for a very long distance, to the middle of the orbit in fact. The lateral strip of this bone bears an ornament of ridges and grooves, deeply cut and of most unusual character. The sculptured strip extends very far forward, but ends posteriorly a little in front of the level of the basitemporal articulation. Steen held that this strip was made by palatine and transverse bones, but the right lower jaw shows a coronoid process in position with respect to the jugal and maxilla, which determines the anterior end of the subtemporal fossa, and thus of the hinder end of the transverse bone ; it lies much too far forward to make Dr. Steen's interpretation plausible. Furthermore, the ridges of the ornament on the presumed " ectopterygoid " continue the direction of those on the pterygoid, as they would be unlikely to do across a suture.



Text-fig. 24.—*Pelion lyelli* Wyman. Reconstruction of a skull (B.M.N.H., R.2674). × 2·2. A, Dorsal ; B, palatal ; C, right lateral aspect. Reference letters as before.

It is thus evident that Dr. Steen (and Dr. Romer) were unjustified in regarding this skull as broad and low, and it remains to determine its shape.

As Steen recognized, the left premaxilla is in position and the series of teeth it supports clearly shown. The parasphenoid—a little laterally bent—is in articulation with the anterior part of the palate, and the dorsal surface of the skull—though the sutures connecting its bones opened a little when it was spread out flat—is essentially intact. It is evident that the part of the pterygoid which on the spectator's right lies mesial of the basicranial articulation is the parotic plate, which in life was essentially vertical.

Thus reconstruction of the skull shape is a matter of fitting measurements so that dorsal, ventral and lateral views are self consistent and provide projected transverse sections which give proper measurements. I began with the right maxilla, jugal and quadratojugal, which show that the lower border of the cheek turns downward from the direction of the straight maxillary border. The otic notch of the left side and upper part of the squamosal in front of it are shown ; they allow the depth of the cheek at its hinder border to be measured, and the size and shape of the right quadratojugal and jugal fix the outline of the squamosal, though there is a possible foreshortening by obliquity in direct side view. The width of the table, between the otic notches, is shown for the left side, the interorbital width and the sizes and shapes of the postfrontal, postorbital, intertemporal and supratemporal are known, and in no Labyrinthodont is the table more than gently curved. Thus trial sections give possible proportions. The skull shape so determined, with its very characteristic down-turning of the lower border of the cheek behind the orbit, was then fitted to the lateral aspect of the lower jaw as shown directly on the animal's right, the jaw being shortened because it is a curved structure which has been laterally flattened into a straight one.

The resulting fit is surprisingly good. Finally the palate has to be fitted in. The distance measured from the most lateral point of the basitemporal facet of the pterygoid to its lateral border is known. The distance from the most dorsal point of the parotic plate to the border of the pterygoid is known. The lowest possible place for the outer border of the pterygoid with respect to the lower jaw is known. Thus trial transverse sections made by measurements of individual bones along correctly determined directions allow small modifications to be made until everything fits. Finally the parasphenoid has to be put into place. The reconstruction of the skull carried to the present point has fixed the position of the facet for articulation of the pterygoid with the parasphenoid. The parasphenoid is still in position with respect to the premaxilla. Direct measurements made on the skull photograph show that the distance from the front point of the interpremaxillary suture to the articular facet on the pterygoid agrees exactly with that for the pterygoid on the parasphenoid, when the measurement is made on a trial longitudinal section of the skull. Thus the slope of the bone in side view is established, the total length from the anterior end of the skull to the hindmost point of the parasphenoid is known, so that the position of the occiput is fixed with considerable certainty. The results are shown in Text-fig. 24. It may be added that there are no traces of any cartilage bones in the brain-case, so that the animal was probably very young.

### PROBABLE RELATIONSHIPS OF PELION

As so restored *Pelion* has notable resemblances to *Eobrachyops*. The two agree in having anteriorly placed orbits and a shallow face, behind which lies a long post-orbital skull with a wide table, cheeks sloping steeply downward, a lower border which passes downward from the hinder end of the short maxilla (at the level of the hindmost point of the orbit) to a low-placed quadrate, and an occiput which slopes backward below the hinder border of the table. The shape of the intertemporal is very much the same in the two animals, which implies that the mutual relations of all the bones in the postorbital region are very similar. In each the interpterygoid vacuity is very large, and the palate deeply vaulted as a result of a great widening of the pterygoid and the down-turning of its lateral strip mesial to the masticatory muscles. *Pelion* and *Eobrachyops* have an identical mode of articulation between the hinder surface of a processus internus of the pterygoid and a vertical facet on the laterally widened anterior border of the parasphenoid. In each animal the lower jaw has a very unusual straight lower border, and an upstanding coronoid process, not including any contribution from the surangular, conditions otherwise unknown in Labyrinthodontia except in *Dvinosaurus* and the Brachyopids. But *Pelion* retains an otic notch, a structure no doubt found in all primitive Labyrinthodonts, but lost in *Eobrachyops, Dvinosaurus* and all other Brachyopids. Thus it is not improbable that *Pelion* is closely related to the ancestry of *Eobrachyops*, and hence to that of *Dvinosaurus* and the Brachyopids.

## EOBRACHYOPS COMPARED WITH ERPETOSAURUS

My attention was called to *Pelion* in this connection by the existence in it of the processus internus of the pterygoid, and, as *Erpetosaurus* has a similar structure, that animal should also be reconsidered.

### DESCRIPTION OF ERPETOSAURUS MATERIAL

Dr. Steen's material includes a skull (*E. radiatus*) in counterpart, so that an imperfect dorsal surface (R.2672) and a wonderfully preserved hinder part of the palate (R. 2670a) are available, together with an interclavicle, vertebrae and scutes (R.2672). A second skull (*E. laevis* B.M.N.H., R.2662) shows a well-preserved ventral surface, of which only the right hinder corner is missing, and another slab (R.2660) contains an interclavicle, scutes and vertebral elements. I have rubber casts of this material for comparison with Dr. Steen's descriptions, and can confirm them, adding something because my casts are so much better than her squeezes.

No. R.2670a retains the impression of the hinder part of the palate of a skull whose dorsal surface is shown by R.2672. This skull has the lower jaw of each side articulated with the quadrate, so that only small parts of this bone are visible. The pterygoids, though broken into parts by cracks, are perfectly preserved in detail and can be restored without difficulty. The ventral surface of the parasphenoid, and left side of the brain-case—much dorsoventrally flattened but otherwise well preserved—are visible, but a short misplaced rib running antero-posteriorly below a lappet belonging to the parasphenoid introduces some difficulties. The basioccipital is perfectly preserved, uncrushed, in articulation with the parasphenoid. The right exoccipital has swung round so that the whole of its posterior surface is shown, whilst the left retains its natural position, but is dorso-ventrally compressed. The parasphenoid is very well shown, and the left stapes is in its natural place.

Thus from enlarged photographs, on which the outlines of all important structures are inked in, it is possible by trial and error to restore the whole occipital region, measurements made directly from the casts with proportional compasses set at the magnification of the photographs giving constant control and guidance. The results are set out in Text-figs. 25 and 26, which in most matters explain themselves, but are here supplemented by notes on some points.

## Brain-case

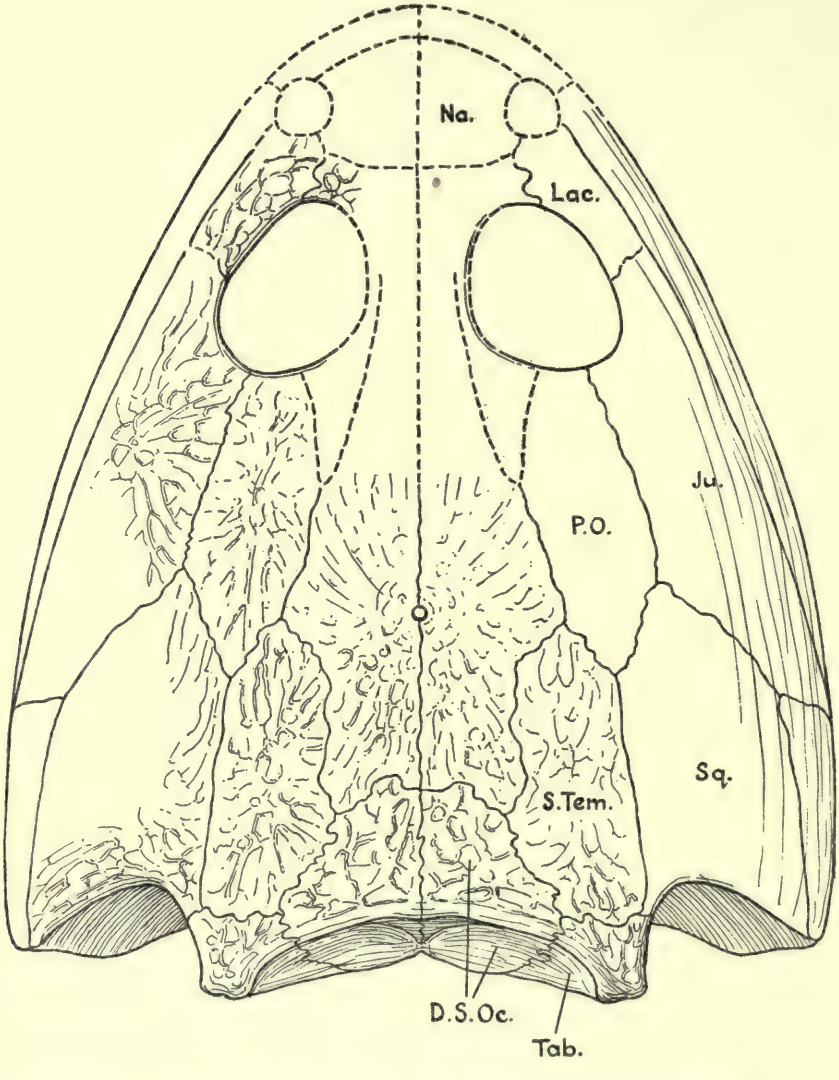
*Occipital condyle.* The large basioccipital has a widened, trumpet-shaped hinder end in front of which the bone narrows until it is surrounded by a ridge on the hinder part of the parasphenoid, which overlaps it at a very obvious denticulated suture. The " condylar surface " is a very deep conical pit. Each exoccipital bears a large concave articular surface lying largely lateral to the foramen magnum, joining the surface by which the exoccipital is attached to the basioccipital.

*Occipital surface.* The exoccipital is a very large thin sheet of bone of elaborate shape. It is evidently mainly perichondral bone sheathing the paroccipital so completely that it stretches far out beyond the vagal foramen, and wraps round the lower surface of the otic capsule, mesial of the fenestra ovalis, so that its anterior border has a long contact with the hinder border of the parasphenoid.

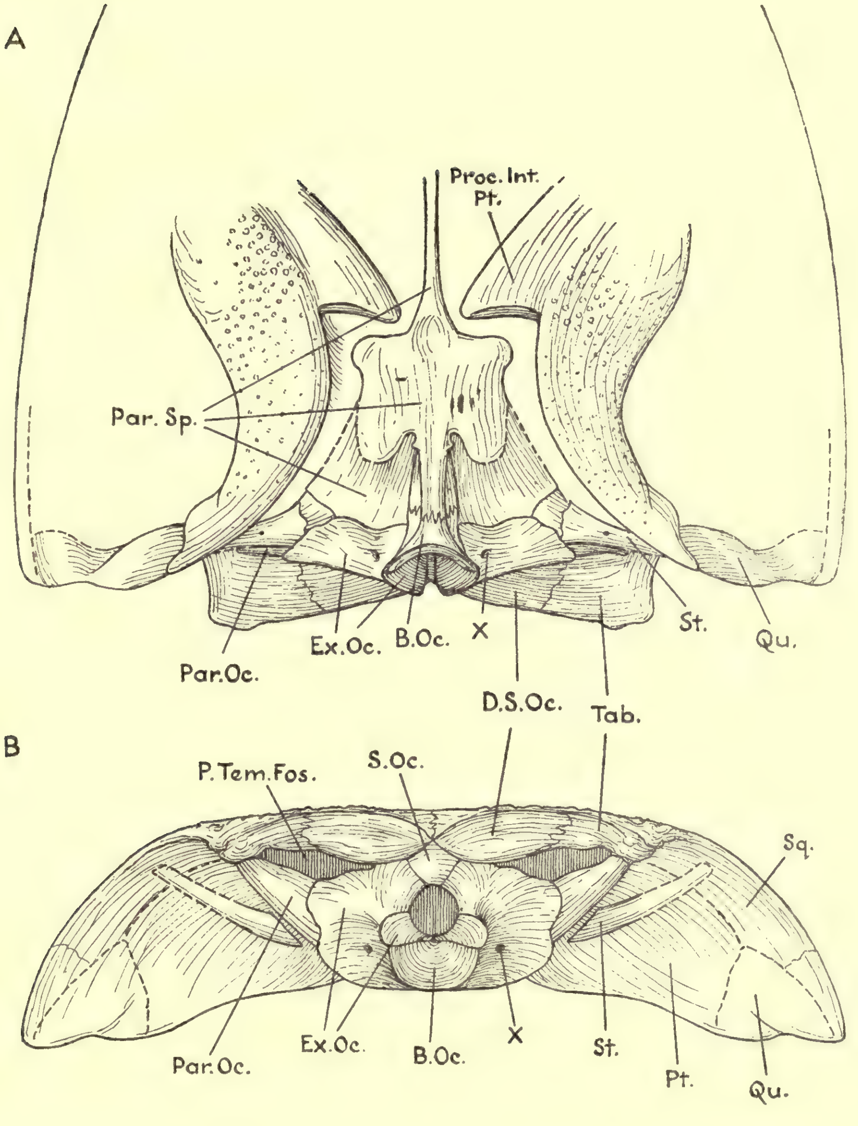
*Supraoccipital.* About one-half of the posterior surface of a supraoccipital showing part of the border of the foramen magnum is seen in articulation with the right exoccipital.

The *parasphenoid* is seen from below, a little hidden by a rib which is overlapped by a free ventral lappet of parasphenoid, and partly concealed on the other (right) side by a displaced ventral scute and fragments of pterygoid. The bone is cracked transversely, the hinder part—when viewed from below—lying some half millimetre dorsal to its original continuation. This is interpreted in Dr. Steen's restoration (text-fig. 1) as a pocket, but is shown by the new cast to be no more than a crack. Behind this fracture the parasphenoid bears a wide median ridge whose ventral surface becomes rounded posteriorly where it sheathes the basioccipital. The sides of this ridge are almost vertical, but pass into the wide lateral expansions of the hinder part of the bone. These pass backward until they meet the anterior borders of the exoccipitals. Lateral to this contact the border passes outward and forward, overlapping the proötic nearly to the border of the fenestra ovalis.

The *paroccipital* is represented only by a completely crushed but bony outer end, lateral to the exoccipital. The left stapes is present in position. It is a powerful bone with a wide flat foot, narrowing rapidly until it plunges under the quadrate


Na.
Lac.
Ju.
P.O.
Sq.
S.Tem.
D.S.Oc.
Tab.

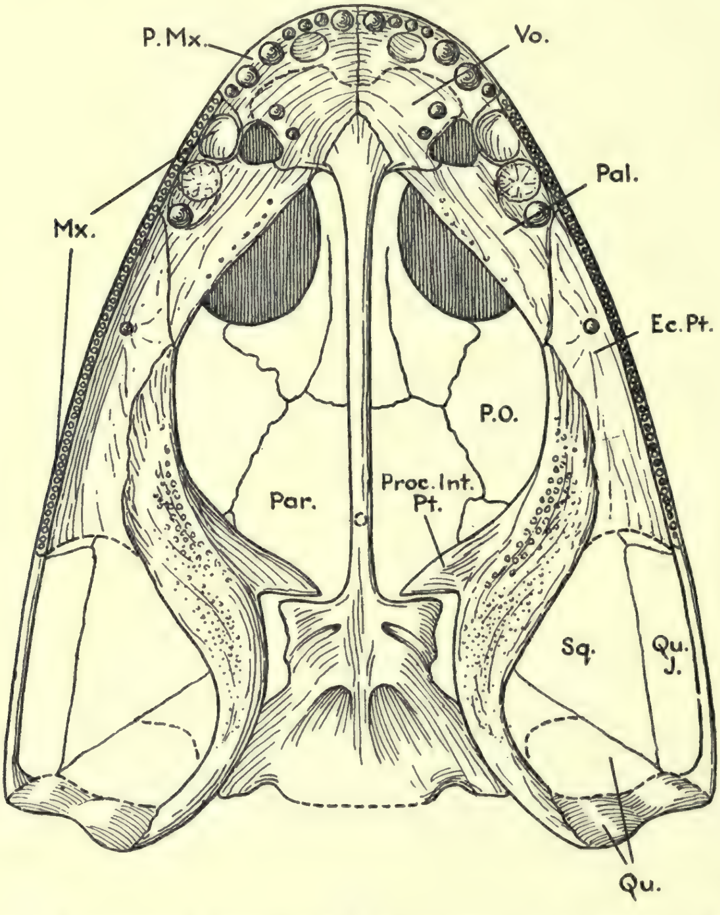
Text-fig. 25.—*Erpetosaurus radiatus*. Reconstruction of a skull (B.M.N.H., R.2670a). × a little more than 2. Dorsal aspect. (Text-fig. 26 is of the same individual.) Reference letters as before.


A
Proc. Int. Pt.
Par. Sp.
Par.Oc.
Ex.Oc.
B.Oc.
X
St.
Qu.
D.S.Oc.
Tab.
B
P.Tem.Fos.
S.Oc.
Sq.
Par.Oc.
Ex.Oc.
B.Oc.
X
St.
Pt.
Qu.

Text-fig. 26.—*Erpetosaurus radiatus* (B.M.N.H., R.2672 and R.2670a). × a little more than 2. Reconstructions A, of the hinder part of the palate, and B, occiput. Reference letters as before.

ramus of the pterygoid and is lost to sight. A very small perforation, presumably for a stapedial artery, enters its ventral surface far laterally.

*Tabular and dermosupraoccipital.* These bones lie largely on the dorsal surface of the table, but posteriorly they are deeply depressed where a pair of muscles spread forward from the neck to overlap small rounded areas. These areas are bounded anteriorly by a step rising to the highly ornamented dorsal surface of the skull, and are largely visible from behind.



TEXT-FIG. 27.—*Erpetosaurus laevis* (B.M.N.H., R.2662). ×2¼ approx. Reconstruction of the palate. The dotted circle in the processus cultriformis of the parasphenoid is the position of the pineal foramen. Reference letters as before.

## PALATE

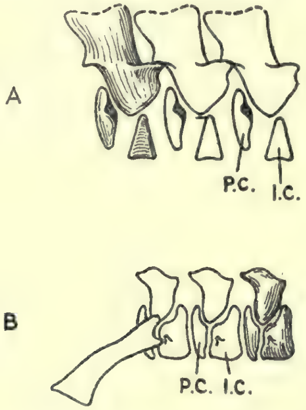
The palate as a whole is shown in *E. laevis* (R.2662), specifically distinguished by Dr. Steen from R.2670a described above. The distinction is valid, the parasphenoid of R.2662 lacking the free lappets of the other animal and bearing two grooves leading to foramina for the carotids, absent in R.2670a. They are, however, similar in all important known characters. R.2662, though well-preserved and nearly complete, is very difficult to interpret because the dentition is most unusual. The maxilla has slid downward and outward over the palatine, and the great premaxillary teeth have crushed forward and outward. Except anteriorly my figure agrees rather better with Dr. Romer's than with Dr. Steen's, whilst the difficult premaxilla is unlike either previous drawing.

## Vertebral Elements

The specimen R.2672 of *Erpetosaurus* has associated with the skull an interclavicle and some other bones, together with some vertebral elements and very many scutes. Dr. Steen has described and figured most of these, but the new cast makes it possible to describe some vertebrae. A single intercentrum is seen end-on as a crescent-shaped bone, exactly like that of *Trimerorhachis.* It is a short segment of a cylinder of bone surrounding a notochord of large diameter and very little constricted. Its visible semicircular border is sharp-edged and a little out-turned. It bears no visible rib attachment. Closely associated are three pleurocentra. They are exposed from their outer surfaces and, except for a transverse fracture of one, show very little evidence of curvature to surround a notochord. They taper a little to each end, and have part of the upper end of one margin everted so as to leave an articular facet directed outward and either forward or backward. The two elements of a single unfused neural arch agree, except that the spine of one stands across the bedding and is crushed down and incompletely shown. The neural arch element has a high spine widening as it passes upward ; its hinder border comes down on to the postzygapophysis, whilst the anterior border is at the root of the anterior zygapophysis. There is no transverse process, or sign of rib articulation. Text-fig. 28, A, is a restoration from these elements.

Another slab from Linton (B.M.N.H., R.2660) shows very many ventral scutes, and part of the inner surface of an interclavicle, which resemble those of *Erpetosaurus*. It is not capable of definite determination, but in many ways agrees with the original (R.2664) of Steen (pl. 4, fig. 2) showing twenty-five or more of the " triangular plates " which she figured. In this specimen the following matters seem certain (*a*) that all the elements are paired, none fused into cresent-shaped intercentra, as is the single example in R.2672 ; (*b*) all these bones have an internal surface toward the notochord which appears granular, and a smooth outer surface ; (*c*) two types are present, intercentra and pleurocentra. An intercentrum widens toward its lower border, which turns in under the notochord but does not meet its fellow, and has a blunt dorsal end. The hinder border is cut into by a rounded depression for surviving cartilage continuous with the neural arch, the rib head being connected by a ligament to a small pimple in the middle of the side of the bone. The other element, a pleurocentrum, is somewhat deeper than the intercentrum, and narrows both above and below. It bears an articular facet cutting into the summit of the anterior border of its smooth outer surface. The neural arch is very poorly shown, though there is an example in articulation with an intercentrum and pleurocentrum (Text-fig. 28, B) ; in no case is there any sign of a transverse process. I can only assume that here and in *Erpetosaurus* the rib articulated with the neural arch and pleurocentrum where the facet existed, and that in the present specimen its other head was tied to the " pimple " without any contact. There is evidence that the rib forks, one of the " heads " having a pointed, non-articular tip. The differences from the *Erpetosaurus* vertebrae already described may well be due to differences along the length of the column.

Thus the structure of *Erpetosaurus* is relatively well known, and its systematic position should be easily determinable. The vertebral column, as Dr. Steen has shown, agrees with that of the contemporary *Stegops*, and is of a type found in the Middle Rothliegende *Acanthostoma*, where as she states (1937 : 499), " both pleura- and intercentra being ossified as right and left hemicylinders, unfused in the mid-dorsal or mid-ventral line." Romer (1947 : 169) doubts this interpretation, suggesting that the intercentra shown in Steen (1937, text-figs. 4 and 5) are twisted round and seen from below. I have examined casts of the specimen and its counterpart, which are not good enough to permit any definite conclusion, but Dr. Steen, with the original slabs before her, is unlikely to have been wrong in such a point.



TEXT-FIG. 28.—A, *Erpetosaurus radiatus* (B.M.N.H., R.2672). Reconstruction from scattered elements of three vertebrae from the right side. The intercentra are single ; B, ?*Erpetosaurus* (B.M.N.H., R.2664). Three vertebrae and a rib from the right. The shaded set of elements is drawn as it actually occurs. The intercentra are paired. All about 2 diameters.

Thus these vertebrae differ from ordinary rhachitomous vertebrae (*a*) in the absence of a transverse process well separated from the parachordal part of the neural arch, (*b*) in the usual existence of paired intercentra, which sheath the notochord for a large part of its circumference, (*c*) in the very high pleurocentra which extend over a very large part of the notochord. They are what Romer (1947 : 64, fig. 11) calls protorhachitomous, which by further ossification could well become embolomerous. *Stegops* is supposed by Romer to be related to *Acanthostoma*, which is evidently close to *Zatrachys*. If these views be justified then we have for the first time direct evidence of the evolution of typical or nearly typical rhachitomous vertebrae from such a protorhachitomous type.

### SIMILARITIES BETWEEN THE TWO FORMS

Thus, except for the processus internus of the pterygoid and its mode of articulation with the parasphenoid, there is in *Erpetosaurus* no resemblance to *Eobrachyops* such as that which *Pelion* shows; but the vertebrae of *Eobrachyops* are " protorhachitomous", comparable with those of *Erpetosaurus* and *Stegops*.

## PLATYSTEGOS LORICATUM Dawson

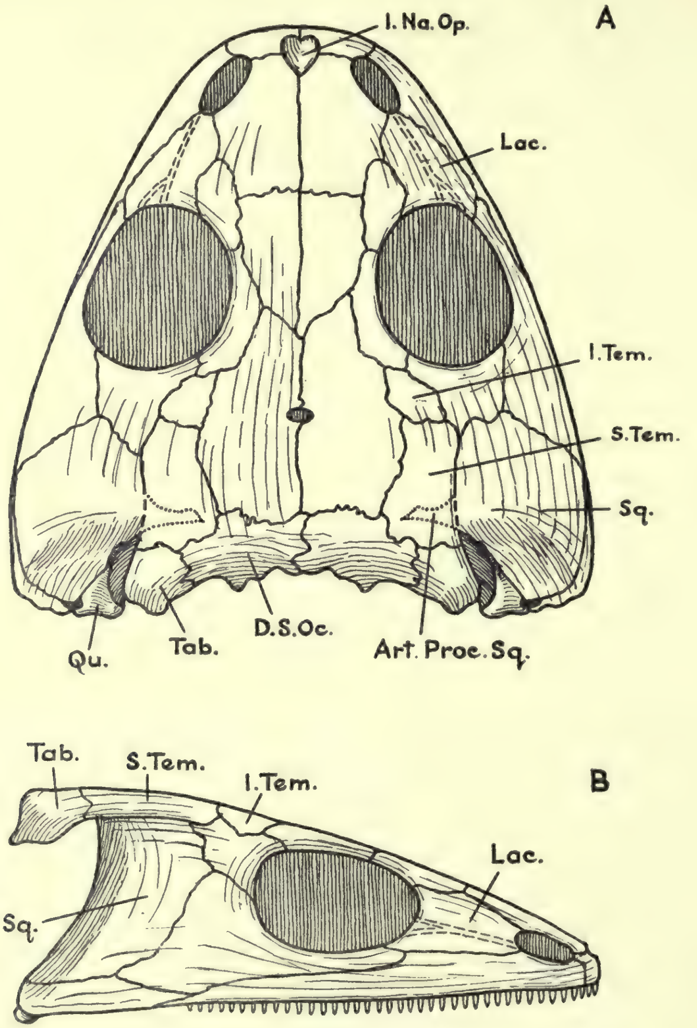
### DESCRIPTION OF MATERIAL

Another, earlier, Labyrinthodont, with a processus internus as a mode of articulation of the pterygoid with the parasphenoid, is an incomplete skull, apparently referable to *Platystegos loricatum* Dawson, from the Coal Measures of South Joggins, Nova Scotia, described by Dr. Steen (1934 : 480, 481). The South Joggins section is thick—11,000 ft. according to Dawson—and the amphibia come from the interior of hollow lepidodendroid trunks which stand on coal seams. Most are from Division IV, Section XV of the section ; this is about half-way up. The evidence of age comes mainly from plants, but according to Bell (1944) they are Westphalian B. Bell noted that the whole series does not extend high enough to reach the first occurrences of *Anthraconauta phillipsi*, but contains molluscs compared to *Anthracomya* cf. *modiolaris*. Thus the series seems to correspond to the Middle Coal Measures of Staffordshire, and the horizon of *Platystegos*, though above that of *Eugyrinus wildi*, is well below that of Linton and Nýřany.

This skull (D.M.S.W., B.95) shows the lower surface of a skull table with the upper part of the right orbit and the face in front of it. The block containing this complex of bones fits on to two others, one of which retains a mould of the lower surface of the table and the hinder parts of the two pterygoids, the left essentially in natural position though forced a little (perhaps 3 mm.) upward, the right misplaced. The third block continues the latter and shows the outer surface of the left side of the skull from premaxilla to quadrate, the quadratojugal being misplaced and lying in the orbit. The right pterygoid extends forward until it overlaps the vomer and palatal bones, whose upper surfaces are shown. The jugal of this side is detached and visible from nearly all aspects. The brain-case is completely missing, but one ramus of the lower jaw is largely seen.

### STRUCTURE OF SKULL

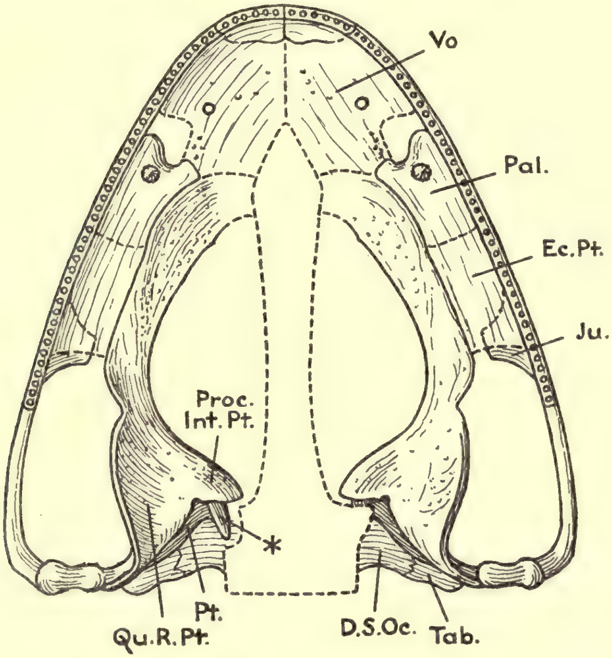
The general structure is clearly shown in the drawings in Text-figs. 29 and 30 which, though restorations, are carefully measured projections based on adequate, undistorted remains. The skull is short and broad, a little less than half its maximum breadth in height. The orbits are large and in the middle of the length, and the otic incision is overhung by the tabular, which forms a short process behind it. The hinder border of the dermosupraoccipitals and tabulars is turned downward, and there is some evidence that the occiput extended considerably behind the table and the quadrate condyles. There is a well-defined scar on the inner surface of that ridge of the tabular which forms the upper border of the tympanic notch which can only have articulated with the end of the paroccipital process. It is thus evident that no process passed inward from the tabular in contact with the upper surface of



Text-fig. 29.—Skull of *Platystegos loricatum* Dawson. (D.M.S.W., B.95) × 1½. Restored drawings of the skull. The sutures on the skull roof are taken from the lower surface. A, Dorsal aspect; B, right side. *Art.Proc.Sq.*, articular process of the squamosal for attachment to the supratemporal; *D.S.Oc.*, dermosupraoccipital; *I.Na.Op.*, internarial opening; *I.Tem.*, intertemporal; *Lac.*, lachrymal; *Qu.*, quadrate; *S.Tem.*, supratemporal; *Sq.*, squamosal; *Tab.*, tabular.

the paroccipital and below the post-temporal fossa. This condition exists in the Loxommids, but has been lost in all other Labyrinthodonts. There is an intertemporal bone separating the supratemporal from the postfrontal, and the lachrymal —which shows the course of the duct with its two canaliculi from the orbit—forms a large part of the orbital margin and the hinder border of the nostril.

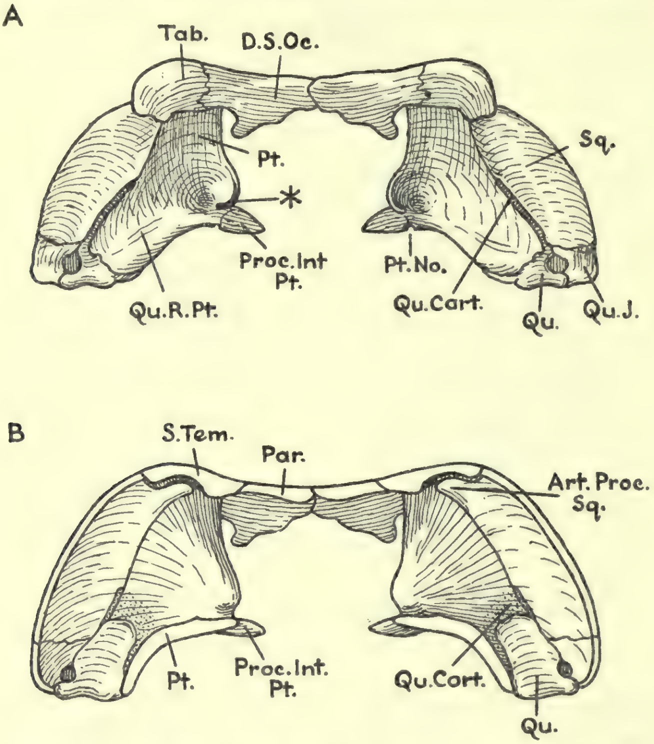
The squamosal is remarkable because it is not attached suturally to the outer margin of the supratemporal. It abuts against it, the bone being 1·5 mm.—or a little more—in thickness in a skull some 5 cm. long. To strengthen this attachment a special process arises from the upper end of the admesial border of the subotic flange of the squamosal; this process passes directly inward with its essentially flat but dimpled upper surface opposed to a special sharply marked depression on the lower surface of the supratemporal. This arrangement, which is seen on both sides of the specimen, implies a powerful, ligamentous attachment.



TEXT-FIG. 30.—Skull of *Platystegos* as in Text-fig. 29. × 1½. Palate. *D.S.Oc.*, dermosupraoccipital; *Ec.Pt.*, ectopterygoid; *Ju.*, jugal; *Pal.*, palatine; *Proc.Int.Pt.*, processus internus of the pterygoid; *Pt.*, pterygoid; *Qu.R.Pt.*, quadrate ramus of pterygoid; *Tab.*, tabular; *Vo.*, vomer; * pterygoid process described in text, p. 381.

The left quadrate is well shown from behind. Its lateral border is notched immediately above the shallow but wide outer condyle by the quadratojugal foramen, and a narrow parallel-sided strip of its posterior surface extends upward, visible between the inner border of the sub-tympanic flange of the squamosal and the hinder border of the parotic flange of the pterygoid. Some distance above the bony quadrate the inner edge of the squamosal steps inward to meet the pterygoid, presumably above a cartilaginous upward extension of the quadrate. There is a considerable pterygoid flange of the quadrate.

The pterygoid is a remarkable bone, not to be matched in any other Labyrinthodont known to me. The attachment to the basis cranii is by a processus internus, whose lower surface is rounded from back to front. This is abruptly truncated by a face which evidently articulated with a flat transverse facet on the parasphenoid. The anterior margin of the process begins at a point mesially and bows forward to its root. It there swings forward to continue as the border of a rather large interpterygoid vacuity. This border can be seen on the right side until it passes below a misplaced lower jaw and cannot be followed. But it is evident that the pterygoid is still wide when it reaches the vomer, and that it may well have reached the para-



Text-fig. 31.—Skull of *Platystegos* as in Text-fig. 29. × 1½. A, Posterior view of the skull, lacking brain-case; B, the posterior part of the skull, without brain-case, cut across about at the middle of the supratemporal and viewed from in front. Cut surfaces are left white. *Art.Proc.Sq.*, process of the squamosal which is applied to the supratemporal; *D.S.Oc.*, dermosupraoccipital; *Par.*, parietal; *Proc.Int.Pt.*, processus internus of the pterygoid; *Pt.*, pterygoid; *Pt.No.*, "notch" in the pterygoid; *Qu.*, quadrate; *Qu.Cart.*, cartilaginous continuation of the quadrate; *Qu.J.*, quadratojugal; *S.Tem.*, supratemporal; *Sq.*, squamosal; *Tab.*, tabular; * pterygoid process described in text, p. 381.

sphenoid. The lower surface of the processus internus continues laterally without break into that of the body of the pterygoid, which lies mesial of the vacuity for the masticatory muscles, and extends down within them to a curved ventral border.

The processus internus lies so far back in the skull that the quadrate ramus is not distinguishable from the body of the bone. The ramus sheathes the pterygoid process of the quadrate, rolling over its ventral border so as to form a rounded transition from the horizontal body to the concave upper part of the quadrate ramus. The quadrate ramus thus sheathes the ventral border and posterior surface of the quadrate, extending forward and inward beyond that bone to rise to the skull roof, behind the articular process of the squamosal. This transversely placed part of the pterygoid has a free admesial border, whose lower end (marked * in Text-figs. 30, 31) —lying above and a little behind the processus internus—projects backward to a point not meeting any other bone. The posterior surface of the pterygoid, between this point, the skull roof and the quadrate, is a hollow cone, incomplete because it lacks a triangular strip of its ventral part between the quadrate and point *. That flange of the pterygoid which sheathes the temporal muscle ends anteriorly by its lower border rising abruptly to pass into the lateral border of the palatal part of the bone. It comes, if not into direct contact with, at least into the very near neighbourhood of, that internal process of the jugal which, as in the majority of Labyrinthodonts, lies dorsal to the ectopterygoid, and often extends behind it to form the anterior border of the subtemporal fossa. The whole palatal surface of the pterygoid seems to have been covered by a sparse granulation of small teeth, little more than hemispherical projections.

No definite part of the ectopterygoid is visible, but the anterior end of the right palatine is well shown from above and from the outer side. The admesial part of the bone is a thin sheet with a feather edge. This passes laterally into an upturned ridge whose lateral face is deep, rounded from dorsal to ventral borders, and longitudinally grooved, evidently in continuous contact with the maxilla. This border ends by sloping down as the upper surface of a deep notch, the hinder border of the palatal nostril. Immediately below this process the bone carried a tusk, circular in section, with a sharply-grooved base. The large vomer is overlapped by the anterior end of the palatine, mesial and anterior to which it has a wavy thin posterior border, presumably articulating with the pterygoid. It is evident that some part of the bone has a granulation of small blunt teeth, widely spaced, and similar to those of the pterygoid. There is evidence of a vomerine tusk placed perhaps mesial of and near to the anterior end of the palatal nostril.

The left premaxilla is present in place, attached to the admesial end of the left maxilla. The anterior part of the internasal opening is shown. The suture with the nasal and the bone's contribution to the border of the nostril are uncertain. Some of the premaxillary and maxillary teeth are shown, and justify the figures. The general shape is certain, as the left side of the skull from front to back is visible, giving no evidence of distortion except for an inturning of the maxillary lower border, and the other drawings are fitted into the space so determined.

The inner surface of the hinder end of the right ramus of the lower jaw is shown from above, and an irregular transverse section of its anterior part is shown on a fractured surface. The face on the articular for the quadrate is fully ossified, divided by a low ridge into inner and outer regions for the quadrate condyle. It is clasped by the surangular laterally, and the prearticular—which sheathes its inner surface and continues behind it to meet the surangular—forms with that bone a ridge on the posterior surface, penetrated by a circular canal presumably for the chorda tympani. The rounded bottom of a groove on the prearticular helps to isolate the ridge, which is unfortunately damaged by a chisel cut, but may have been a first beginning of a retroarticular process. In front of the condyle the upper border of the prearticular descends very rapidly so as to leave the cavity of the jaw widely exposed from within. Anteriorly, below the orbit, the jaw becomes shallow, nearly as wide as it is high, with a marginal row of teeth bounding a flat upper surface. Thus it is possible that the Labyrinthodont jaws from South Joggins, recognized by Dr. Steen (1934 : 487) as those which first exhibit the later Labyrinthodont retroarticular process, belong to *Platystegos*.

## Comparison with Dendrerpeton and Eugyrinus

*Platystegos* is found with *Dendrerpeton* and a series of very similar forms described by Dawson and Dr. Steen. The proportions, safely determined in each case, show that they may reasonably be generically distinguished. But the two animals are very similar ; the pattern of the external skull bones is essentially the same, the general nature of the palate with its large interpterygoid vacuities apparently bounded by the pterygoids and parasphenoids alone is not too dissimilar, and a processus internus of the pterygoid articulates with the parasphenoid in each. In each the tabular has a descending process from its under surface behind the tympanic space, and the general outline of the ventral borders of the descending flanges of the tabulars and dermosupraoccipitals is similar. In each form, if we may judge *Dendrerpeton* by Steen's photograph (pl. 1, fig. 2) the subotic flange of the squamosal passes smoothly over a rounded surface to the outer side of the skull, there being no well-defined crest as a border to which the tympanic membrane could have been attached. The pterygoid of *Dendrerpeton* is not known to have the extraordinary conical form of the quadrate ramus which occurs in *Platystegos*, but it extends up to the skull roof (Steen, text-fig. 2g) in the same way, and there is evidence in B.M.N.H., R.4553 and R.4554 that the special process of the squamosal which supplements the straight abutment of that bone on the table in *Platystegos* actually occurs in much the same form.

The lack of an interdigitated suture between the squamosal and the skull table in Dendrerpetonts, whilst all other dermal skull bones are firmly attached in that manner, seems to show that the contact itself is of recent introduction into their structure, the development of the special articular process of the squamosal showing that a firm connection is desirable. Similarly in Anthracosaurs the squamosal alone of dermal skull bones fails to have a sutural attachment to the table, and is held in place by the intervention of the palatoquadrate cartilage. The only explanation of the long delay in the establishment of this connection so implied is the survival in their Osteolepid ancestors to a relatively recent period of the notch between the membrane bones of the cheek and table which existed in them.

The group of Dendrerpetonts is additionally characterized by the occurrence of bony scales, oval or shield-shaped, with a delicate concentric striation, together with faint radial striae. In many ways *Platystegos* recalls *Eugyrinus* (Watson, 1940 : 215) which is somewhat older and much smaller. The general pattern of the dermal skull bones is common to the two, though *Eugyrinus* possesses lateral line grooves, apparently absent in all Dendrerpetonts. Both have large occipital flanges from the tabulars and dermosupraoccipitals, and the large parotic flange of the pterygoid reaches the skull roof behind a special articular process of the squamosal in the same way. The mode of articulation of the pterygoid with the basis cranii is different, *Eugyrinus* not possessing a typical " internal process ", and rather resembling *Eryops*. *Eugyrinus* has a " pterygoid flange " against the lower jaw absent in *Platystegos*. The dermal scales of *Eugyrinus* have a general resemblance to those of Dendrerpetonts. But in their possession of large interpterygoid vacuities the two groups agree, differing very greatly from the contemporary Loxommids.

## COMPARISON WITH BRACHYOPIDS

*Eobrachyops* is, for its time, of very advanced and specialized structure. It retains an intertemporal bone and has thus a skull pattern of normal early Labyrinthodont type. But its face is extremely flattened, and its temporal region deepened immensely. The mechanical effect is to enable the animal to open its mouth to an extraordinary extent, by the action of a musculus depressor mandibuli attached to a retroarticular process much longer than in any contemporary. The long temporalis muscle would secure a powerful snapping bite. The wide and deep arch along the palate, between the pterygoid flanges which pass down mesially to the temporal muscle, would enable a large prey to be swallowed and could house a large tongue. The sloping occiput is associated with a very posteriorly-placed condyle, and perhaps with the possibility of raising the head nearly vertical to the vertebral column, and the considerable area of membrane bone on the occiput provides for the attachment of powerful neck muscles.

The stapes of Brachyopids, known in *Batrachosuchus* and *Dvinosaurus*, is presumably a modification of the normal Labyrinthodont type, subsequent to the suppression of the tympanic membrane which must have existed in their ancestors if they were to possess a stapes at all. This loss of an otic notch is associated with a movement back of the point of contact of the squamosal with the skull roof, and involves a corresponding backgrowth of the parotic part of the pterygoid. In association with this change in shape a horizontal flange, essentially a development of the base of the processus internus, comes to arise abruptly from the inner surface of the pterygoid ; separating the parotic plate from that which sheathes the masticatory muscles almost down to their attachment to the mandible.

The quadrate is unique. Its flat inner surface is completely covered by the pterygoid, but the bone itself is exposed as a narrow vertical rib between the pterygoid and the admesial border of the squamosal. Laterally to the quadrate rib the squamosal forms a vertical hollow cylindrical face before passing over a rounded surface to the cheek.

Inspection of the figures of *Platystegos* will show that in many ways it makes a starting point from which the Brachyopids could have arisen. A deep ridge of quadrate is visible from behind between the pterygoid and squamosal, which turns a very little backward towards it. The posterior face is widely and shallowly grooved from top to bottom and it passes over a rounded surface to the outer side, there being no sharply defined ridge for the attachment of a tympanic membrane. The conditions differ from those in Brachyopids in the retention of a definite pterygoid ramus of the quadrate and of the pterygoid sheathing it. But these are common early Labyrinthodont features, which must certainly have existed in some ancestral Brachyopid.

The palate of *Platystegos* has, in the deep flange of the pterygoid which sheathes the masticatory muscles, a structure which alone could have provided the starting point of the Brachyopid condition. The mode of articulation of the pterygoid with the parasphenoid is the same in *Platystegos* and *Eobrachyops*, and the large interpterygoid vacuities provide conditions from which the relatively enormous vacuity of *Eobrachyops* could have arisen long before it is parallelled in most other Labyrinthodonts. It is, of course, most improbable that *Platystegos* is a real ancestor of the Brachyopids: all that can be claimed for it is that in some ways it possesses structural qualities which explain how those which characterize that group may have arisen. On the other hand *Platystegos* differs as completely as any Labyrinthodont can from *Erpetosaurus*, which seems to have been a rapidly advanced form with no known descendants.

*Platystegos* is also important because with its associated Dendrerpetonts and *Eugyrinus* it is the earliest known normal Labyrinthodont, other than the Loxommids, which retains obviously more primitive features in many structures in the skull, together with certain special peculiarities, and an advance in the mode of attachment of the squamosal to the table.

## SURVEY OF BRACHYOPID LINE

We have thus by consideration of the structure of skulls (and lower jaws when they are known) reached the conclusion that *Eobrachyops townendae*, Clear Fork; *Eobrachyops casei*, Clear Fork; *Bothriceps australis*, ? M. Permian; *Dvinosaurus*, U. Permian; *Trucheosaurus*, U. Permian; *Brachyops*, Permo-Triassic boundary; *Batrachosuchus browni*, L. Trias; *Batrachosuchus watsoni*, L. Trias; "*Platyceps*" *wilkinsoni*, L. Trias; *Plagiosternum granulosum*, M. Trias; *Plagiosuchus*, M. Trias; *Gerrothorax*, U. Trias and Rhaetic; and *Plagiosaurus depressus*, ? Rhaetic; are members of a group of Labyrinthodonts relatively closely allied to one another, though not members of a single lineage. These come from Texas, Australia, Russia, India, South Africa, Germany and Sweden, and members of the group are known also from Argentina, Siberia and Spitsbergen. But ten species are known by a single specimen only, two from about three specimens each, and only *Dvinosaurus* is represented by a satisfactory suite of some seventeen. Such a mode of occurrence suggests that the evolutionary history of the group was complex, and the occasional recognizable existence of neoteny emphasises the probability. Furthermore, nothing in the known structure of a single young skull referred to *Pelion* from the Coal Measures of Ohio prevents its acceptance as an early member of the group, but it differs in some ways which will require discussion.

Thus it is evidently impossible to hope to find a true evolutionary series amongst these animals; the whole group would probably have included a large number of species representing not only members of main stocks, but many blind-ended side-branches like *Dvinosaurus*, retaining, when sexually mature, larval qualities which may be (or may, like a frog's tadpole, not be) proper to a time earlier than that in which they lived.

Thus all we can do is to study the group as a whole, placing its members in order of time and recognizing such changes in structure as persist over all or some part of the long life of the stock. I did this (so far as the material allowed) in 1919 (p. 56) showing that the direction of change in structure was the same as in the Capitosaur-shaped skulls from *Eryops* to *Cyclotosaurus*.

The greatly extended knowledge contained in the present paper confirms that conclusion and extends it:

(1) The large mainly basioccipital condyle of *Eobrachyops* passes to the wide, tripartite condyle of *Dvinosaurus*, and that passes to the separated exoccipital condyles and absence of a basioccipital in *Batrachosuchus*, etc.

(2) The ossified supraoccipital of *Eobrachyops* and *Dvinosaurus* vanishes in the later forms.

(3) The widespread exoccipital of *Eobrachyops*, although reaching the tabular, does not extend forward to the pterygoid as it does to an increasing extent in *Bothriceps*, *Batrachosuchus* and the " Plagiosaurs ". The otic capsule contains no visible ossification in any form.

(4) The pterygoid, movably articulated with the parasphenoid in *Eobrachyops* and *Dvinosaurus*, gains a sutural attachment to the lateral border of the parasphenoid in *Bothriceps*, which steadily increases in extent by spreading backward to the exoccipital.

(5) Hypoglossal foramina perforate the exoccipital of *Eobrachyops*, lie on the lateral surface of that bone in *Bothriceps*, emerge through the hinder surface in *Batrachosuchus*, and have disappeared in *Gerrothorax*.

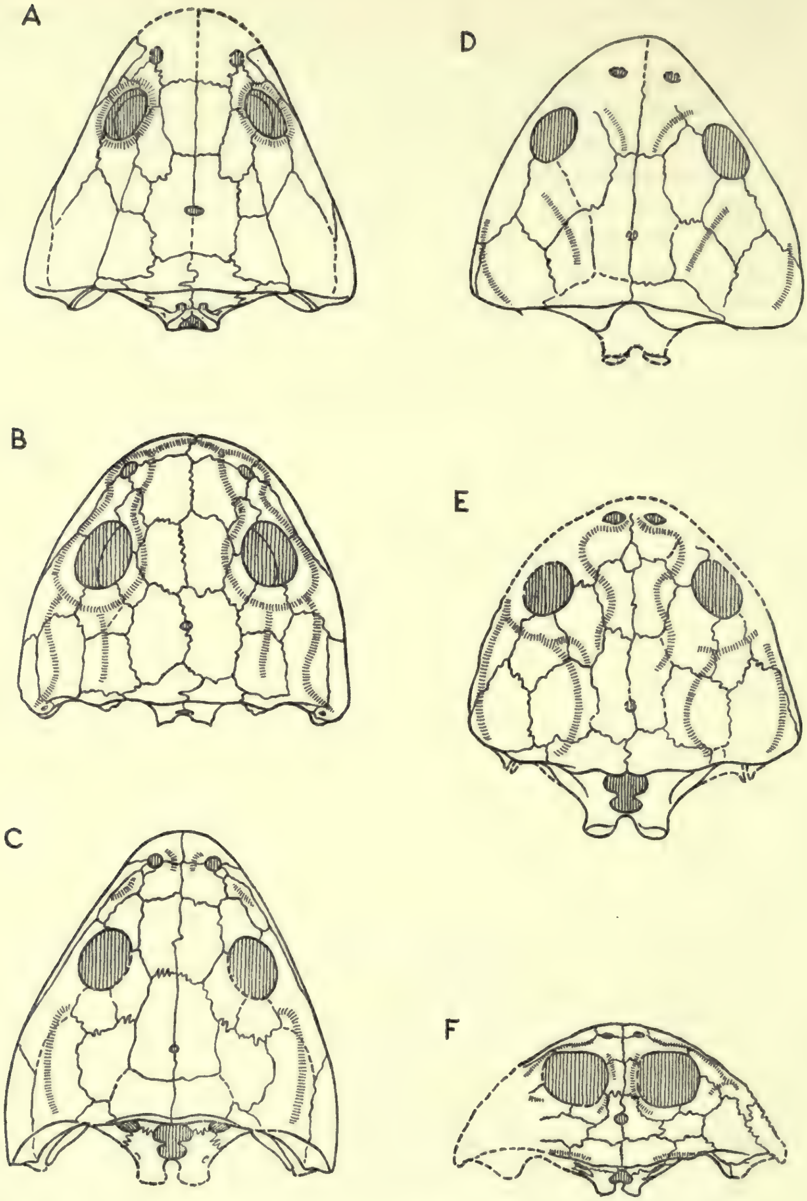
(6) The occipital aspect of the skull of *Eobrachyops* shows a deep occiput and very ventrally placed quadrate condyles. *Bothriceps*, *Batrachosuchus* and *Gerrothorax* show a progressive flattening, both of the lateral suspensory parts of the skull and of the occiput.

(7) The quadrate, which in *Eobrachyops* is on the level of the occipital condyle when the skull is viewed laterally, moves forward in late forms like *Batrachosuchus* and *Gerrothorax*.

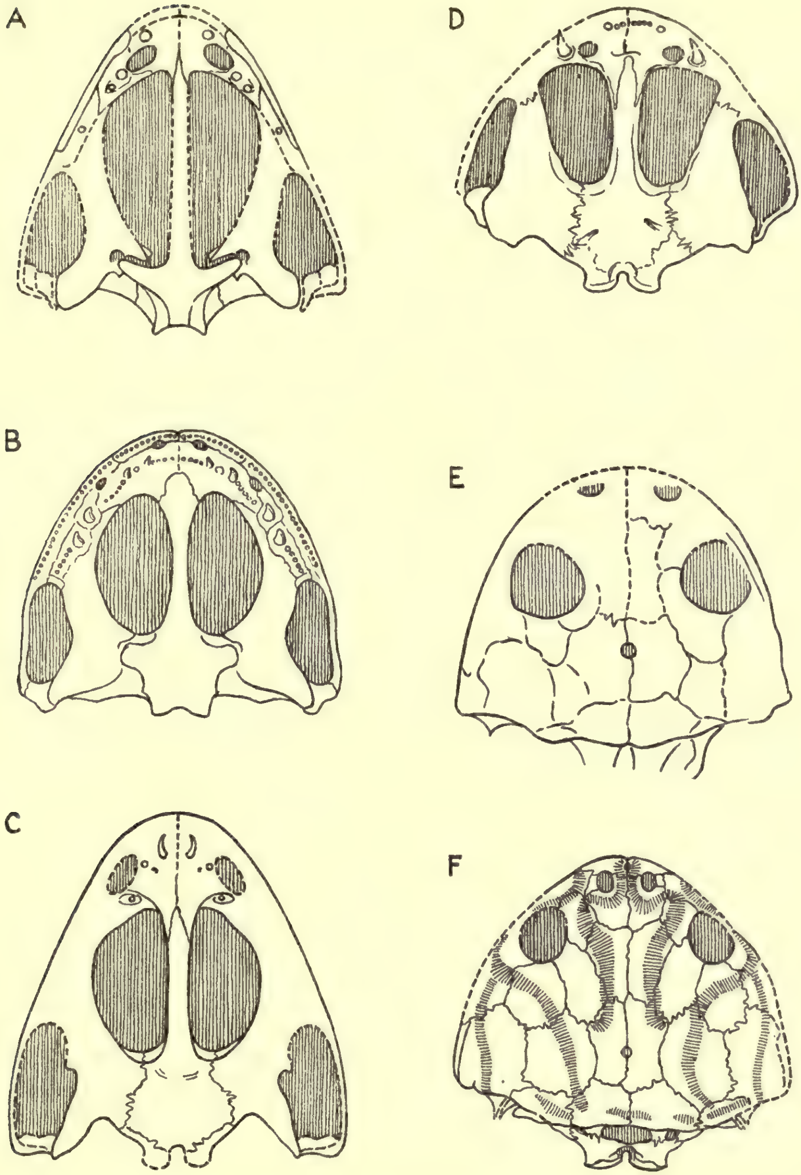
(8) The interpterygoid vacuities of *Eobrachyops* are of very great size, and there is no real possibility of their increase in later members of the group.

(9) The retroarticular process of the lower jaw, present in *Eobrachyops*, considerable in *Bothriceps*, becomes large in *Batrachosuchus* and immense in *Plagiosuchus*.

(10) The intertemporal, present as an independent bone in *Eobrachyops*, fuses with the postorbital in *Dvinosaurus* and vanishes in *Batrachosuchus* and all later forms,



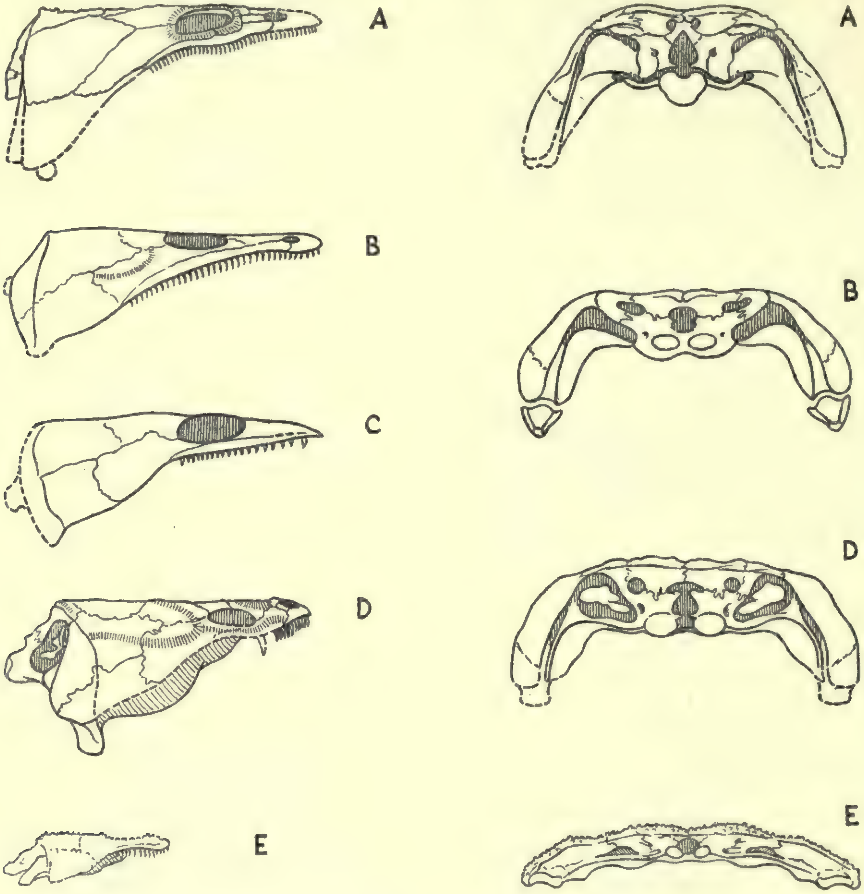
TEXT-FIG. 32.—A series of Brachyopid skulls reduced to the same width. Various magnifications. Dorsal aspects of A, *Eobrachyops townendae*, L. Permian; B, *Dvinosaurus*, U. Permian; C, *Bothriceps australis*, ? M. Permian; D, *Brachyops*, Permo-Triassic boundary; E, *Batrachosuchus browni*, L. Trias; F, *Gerrothorax pulcherrimus*, U. Trias.



TEXT-FIG. 33.—A series of Brachyopid skulls reduced to the same width, various magnifications. Palatal views of A, *Eobrachyops townendae*; B, *Dvinosaurus*; C, *Bothriceps*; D, *Batrachosuchus watsoni*. E–F, Dorsal views of E, "*Platyceps*" *wilkinsoni*; F, *Batrachosuchus watsoni*.

the supratemporal thus coming into contact with the postfrontal, as in rhachitomous and stereospondylous Labyrinthodonts in general.

(11) *Eobrachyops* has protorhachitomous vertebrae, in *Dvinosaurus* they are rhachitomous, though the first vertebra lacks a pleurocentrum, and that of the next two fuses with the intercentrum and neural arch. In Plagiosaurs the neural arch and intercentrum alone remain, the latter bone taking on the appearance of a centrum.



Text-fig. 34.—A series of Brachyopid skulls reduced to the same width, various magnifications. Left-hand column lateral aspects, right-hand column occipital views. A, *Eobrachyops townendae* ; B, *Bothriceps australis* ; C, *Brachyops* ; D, *Batrachosuchus watsoni* ; E, *Gerrothorax pulcherrimus*.

Thus in all important matters the course of evolutionary change in Brachyopids is uniform in direction over the immensely long history of the group, and is the same fundamentally as that found in the Capitosaur relatives.

This paper was begun during the war years, carried further in the late 1940's and

finally written in University College in 1954. All the drawings, which are reconstructions based on careful measurements made from adequate materials, were made by Miss J. Townend after detailed discussions, extending over very long periods, of the significance of all visible details, and the text owes much to her suggestions.

I am indebted to the Royal Society for enabling Miss Townend to work with me, and to University College, London, and Professor Medawar for their hospitality to Miss Townend and myself. The departmental staff deserve our thanks, and we owe much to the splendid photographs made by Mr. W. H. Brackenbury on which our restorations are often based.

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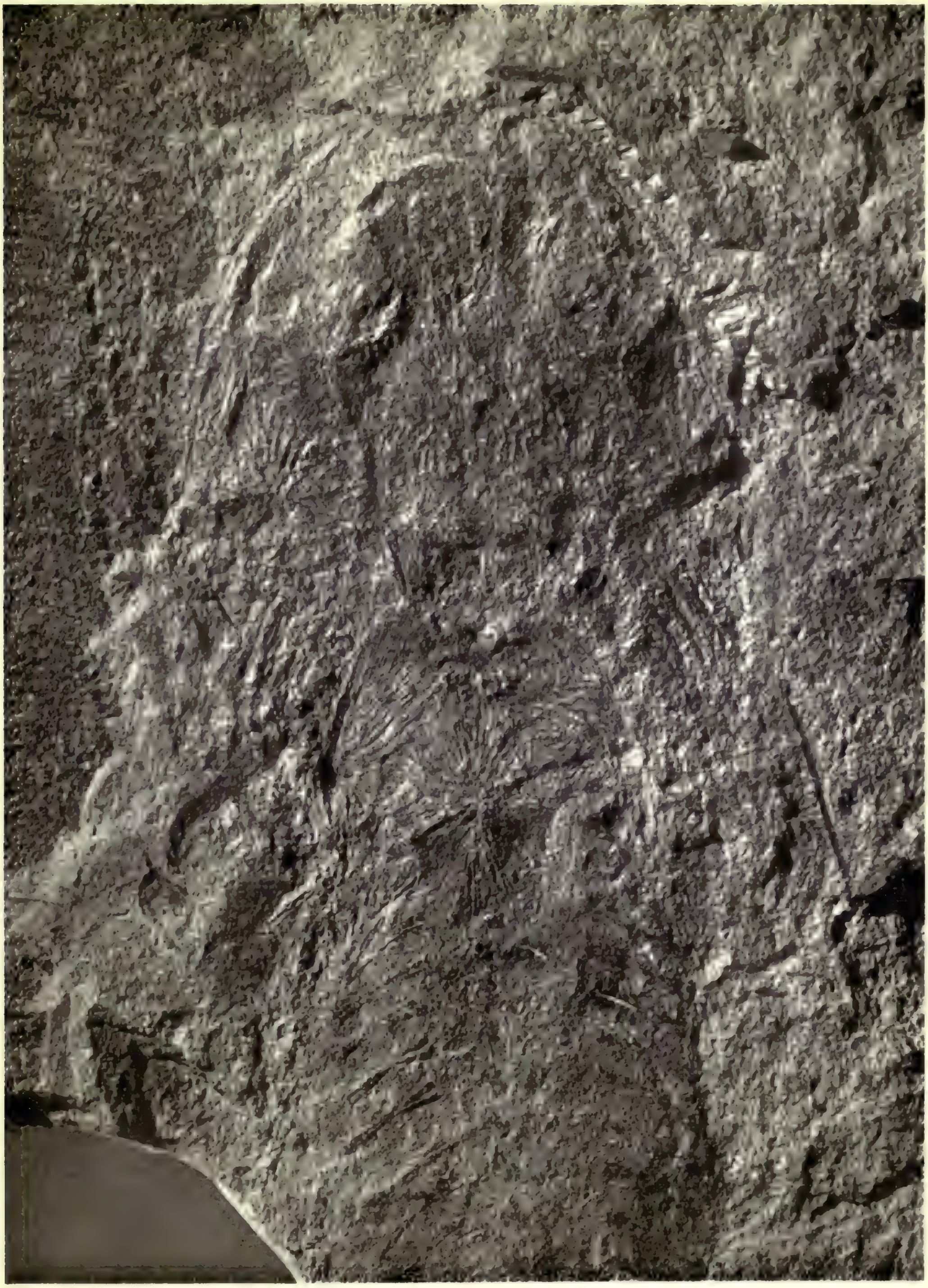
## EXPLANATION OF PLATE 39

"*Platyceps*" *wilkinsoni* Stephens, type specimen. × 3. Narrabeen beds, Gosford, New South Wales. Property of the N.S.W. Geological Survey, Sydney, Australia. (Compare outline Text-fig. 11.)



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